Spatiotemporal Associations Between Forests Impacted By Mountain Pine Beetle And Adjacent Replantings Impacted By Warren Root Collar Weevil

Matthew D. Klingenberg

B.Sc., Redeemer University College, 2006

Thesis Submitted In Partial Fulfillment Of

The Requirements For The Degree Of

Master Of Science

In

Natural Resources And Environmental Studies

(Biology)

The University Of Northern British Columbia

August 2008

Your file Votre référence
ISBN: 978-0-494-48764-8
Our file Notre référence
ISBN: 978-0-494-48764-8

ABSTRACT

A concern to reforestation efforts following the recent outbreak of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is the migration of the below-ground herbivore Warren root collar weevil, *Hylobius warreni* Wood, from stands with a high percentage (>80%) of mature, dead lodgepole pine, *Pinus contorta* var *latifolia* Dougl. ex. Loud., into adjacent young, replanted stands, resulting in significant levels of mortality to juvenile trees. The effects of the spatial patterns of salvage harvesting following outbreaks of mountain pine beetle on the development of Warren root collar weevil pressure in neighbouring, regenerating stands was examined in young lodgepole pine stands in the central interior of British Columbia, Canada. Gradients of tree mortality caused by feeding of Warren root collar weevils were observed and found to be dependent on characteristics of the adjacent, unsalvaged stands. Mortality was exacerbated by high components of dead pine in these stands, and became worse over time. To investigate whether reduced host availability is a potential causal factor explaining such patterns, I constructed three research plots consisting of combinations of live tree, dead tree and mixed (i.e., live and dead) tree habitats and observed dispersal patterns of labelled insects. Weevils were more likely to be captured close to the release location in the mixed and live habitats vs. the dead habitat. Movement rate was high in the dead habitat compared with the live and mixed habitats. In the plot with the dead habitat adjacent to the location of release, the probability of capture was lower, but movement rate and dispersal distance were greater, indicating that Warren root collar weevils will disperse out of a habitat with dead trees into a habitat with live trees. Implications to reforestation strategies following savage harvesting are discussed.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

I would like to first thank Dr. Brian Aukema for welcoming me to work with him over the last two years; it has been a great experience. Thank you for your encouragement of my academic aspirations, attention for detail, and your excitement for the intricacies of forest entomology. Thank you Dr. Gary Chiang and Mrs. Jenifer Chiang from Redeemer University College for teaching me the fundamentals of science, and encouraging me to continue on with my studies. Thanks to the members of the "LAPH" forest entomology research cluster (laboratories of B. Staffan Lindgren, Brian H. Aukema, Lisa M. Poirier and Dezene P.W. Huber) at the University of Northern British Columbia for your discerning ears and fruitful discussions. I would specifically like to thank Dr. Staffan Lindgren for his help with my project over the last two years. Your vast experience with Warren root collar weevils and forest entomology has been vital for making my research possible. I would also like to thank my other committee members, Michael Gillingham and Roger Wheate, for their support throughout the process of my masters, and Dr. Lorraine Maclauchlan of the British Columbia Ministry of Forests and Range for serving as external examiner. Thanks to Ken White and Carolyn Stevens from the British Columbia Ministry of Forests and Range for their help with site selection. Thanks to Rita Wagner and staff at the Prince George Tree Improvement Station for their support. Thanks to Margie Blair from west Fraser Mills for helping me find sites in the Quesnel Forest District. I would like to thank the following people for their technical help with my research projects: Sandy Allen, Hollie Moore, Talya Truant, Gareth Hopkins, Jeff Selesnic, Sean Henderson, and Chris Baker. I also would like to thank Fraser McKee and Honey Giroday for being such an encouragement over the last two years working in the LASER lab. I will miss your camaraderie. I would like to

especially thank my parents, Garry and Ruth Klingenberg, for being supportive and encouraging over the last two years. Finally, I would like to thank the following sources of monetary support: British Columbia Forest Science Program project M086046, the Canadian Forest Service, and Pacific Forestry Centre Graduate, Canfor Graduate, and UNBC Graduate awards.

1: INTRODUCTION

The central interior of British Columbia is experiencing the largest outbreak of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in recorded history (Aukema et al. 2006), which has had an enormous impact on the forest landscape. Large insect outbreaks frequently alter plant-animal interactions within forest ecosystems (Matsuoka et al. 2001), and not surprisingly this outbreak has had an enormous impact on the forest landscape. Now that the recent outbreak has largely run its course, salvage operations and regeneration efforts of affected areas are underway. A significant threat to regeneration following the mountain pine beetle epidemic is the migration of Warren root collar weevils, *Hylobius warreni* Wood, from areas with high percentages of dead lodgepole pine into nearby juvenile stands.

Below-ground herbivory by insects is a concern to the health of young trees throughout North America and Northern Europe (Hunter 2001). Many weevils in the genus *Hylobius* (Coleoptera: Curculionidae) are of particular concern in conifer plantations. A vast amount of research has been conducted on the ecology and management of *Hylobius pales* and *H. radicis* in north-eastern United States (Rieske and Raffa 1990; Rieske and Raffa 1999) as well as *H. abietis* in northern Europe (Nordlander et al. 1997; Månsson and Schlyter 2004; Bylund et al. 2004; Wallertz et al. 2006; Toivonen and Viiri 2006). Less research has been conducted on *H. warreni*. The life cycles and management challenges are relatively similar among species, and research on *H. pales, H. radicis*, and *H. abietis* may be helpful for informing research strategies for *H. warreni*.

Warren root collar weevil is found throughout the boreal forests of North America, feeding on a variety of conifer tree species (Fig. 1.1). Adults are flightless throughout their entire life cycle. Adult females lay up to 25 eggs a year in the duff layer around the root

collar of live trees (Fig. 1.2) (Cerezke 1994). When the larvae emerge, they feed on the phloem tissues of the root collar protected by a hard casing consisting of a mix of frass and tree resin (Cerezke 1970). After two years of feeding at the root collar, larvae pupate and adults emerge (Fig. 1.3). In the early summer months, adults feed nocturnally on young shoots of coniferous trees in preparation for mating and oviposition.

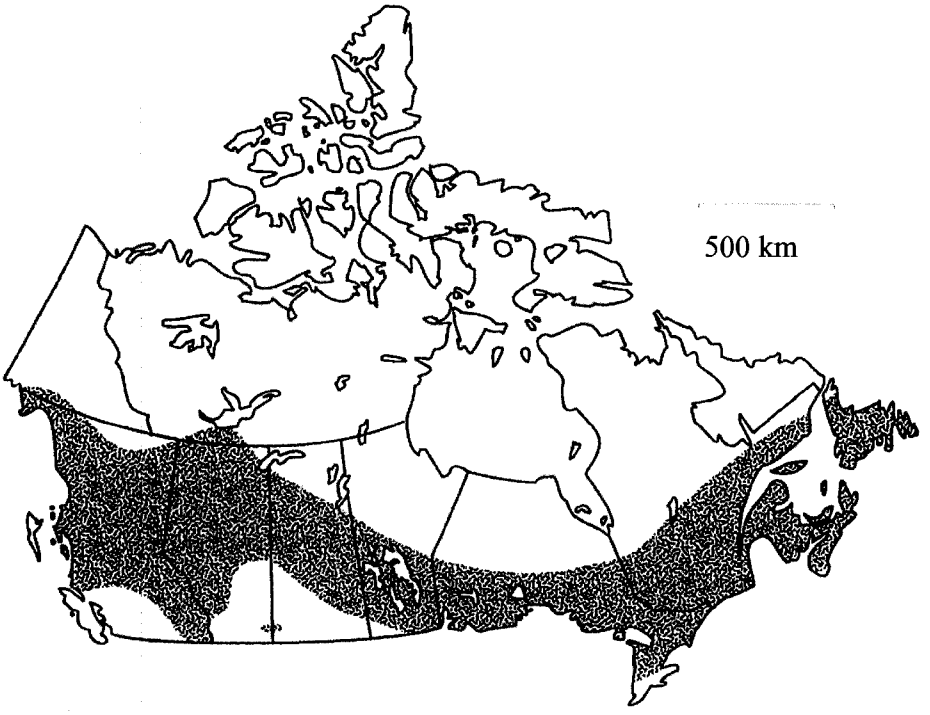


Figure 1.1. Probable range of *Hylobius warreni* in Canada. Adapted and reprinted with permission from Cerezke (1994).

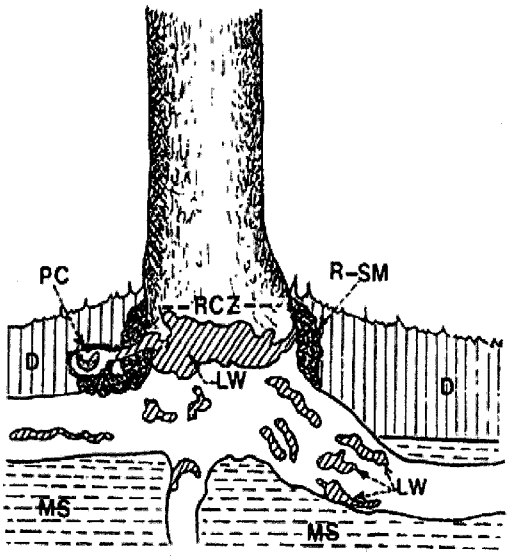


Figure 1.2. Profile of tree base and lateral roots showing the feeding universe of *Hylobius warreni* larvae by the presence of accumulated wounds, position of the pupal chamber away from tree base, duff layer, and resin accumulation. Abbreviations: D, duff; LW, larval wound; MS, mineral soil; PC, pupal chamber with larvae; RCZ, root collar zone; R-SM, resin – soil mass. Adapted and reprinted with permission from Cerezke (1994).

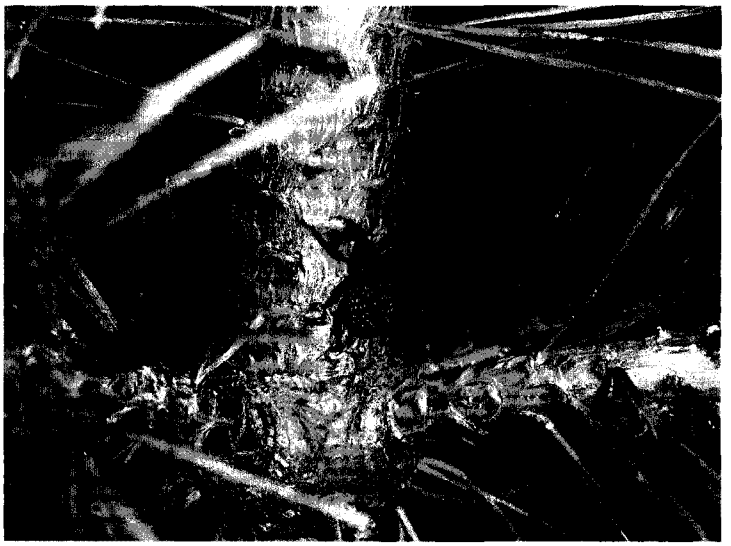


Figure 1.3. Adult Warren root collar weevil on a lodgepole pine seedling. (Photo by MDK)

Forest health issues with Warren root collar weevils are predominately related to larval feeding on young trees. Adult feeding is not detrimental to the host tree, but larval feeding may inhibit growth or even result in tree death (Cerezke 1994). Larval feeding at the base of young trees may girdle the stem, disrupting translocation and killing the tree (Cerezke 1974). Following harvesting, larvae and eggs remaining on residual stumps and root collars mature within the regenerating stands for two years, after which a population is maintained throughout the life of the stand (Cerezke 1973). Rates of tree survival may be complicated by root deformation resulting from planting practices (Robert and Lindgren 2006), as well as by root rots introduced at weevil feeding scars (Whitney 1961; Whitney 1962). Root deformation causes trees to be more susceptible and less likely to survive feeding by Warren root collar weevil, while root rot may kill trees only injured by weevil feeding.

Populations of Warren root collar weevils within regenerating stands are influenced by specific site factors and conditions created during tree harvesting. Harvesting produces slash, which may increase duff depth, favouring the development of weevil populations (Cerezke 1994). The common practice of pre-commercial thinning may also increase weevil numbers per tree, resulting in higher levels of weevil-induced injury (Cerezke 1994). Open site conditions generated within cutblocks may increase soil temperatures around the bases of trees, also favouring insect development (Cerezke 1994). Increased moisture, resulting from rising water table levels associated with extensive tree mortality in stands killed by mountain pine beetle, may also favour the development of weevils within young regenerating cutblocks, because Warren root collar weevils generally prefer moist sites.

Warren root collar weevil has become a concern to forest health in the central interior of British Columbia because adults are depositing eggs on trees that are too small to survive extensive larval feeding, resulting in a high percentage of young seedlings, approximately 4-

12 years of age, being killed. Recent observations of young stands in the central interior of British Columbia have shown cumulative mortality levels as high as 16% (Schroff et al. 2006). Preliminary observations (Ken White, BCMoF) and known biology of Warren root collar weevils (Cerezke 1994) indicate that adult weevils may migrate from areas with high percentages of dead lodgepole pine (>80%) and concentrate in adjacent regenerating cutblocks, increasing the percentage of young trees killed following the recent mountain pine beetle epidemic. Because these weevils feed on all life stages of lodgepole pine and mountain pine beetle has killed most trees greater than 20 years of age, the weevils that were previously feeding on large trees may migrate away from these areas with reduced food resources into adjacent cutblocks.

This thesis investigates the relationship between stands killed by mountain pine beetle and the spatial dynamics of pressure exerted by Warren root collar weevils in young regenerating stands. The findings of this project provide a better understanding of Warren root collar weevil biology and elucidate how this insect fits into the ecology of managed forests in the central interior of British Columbia. These weevils induce significant levels of mortality to young trees and may become a concern for forest managers by limiting the ability of stands to reach "free-to-grow" status. Information generated by this project will complement current strategies as well as outline new strategies to limit reforestation problems associated with Warren root collar weevil pressure (Herring and Coates 1981; Byford 1994).

In Chapter 2, the levels of Warren root collar weevil attack and tree mortality in cutblocks adjacent to stands killed by mountain pine beetle are examined. Warren root collar weevil attack and resulting tree mortality were quantified using 8- x8-m intensive sampling plots, 100-m transects and aerial photographs of entire cutblocks. In Chapter 3, movement

patterns and host preference of Warren root collar weevil are characterized using a bioassay designed to mirror natural field conditions to infer processes that may be generating observed patterns of host mortality in the field. Weevil movement was recorded over a 28-day period through 3 research plots containing various combinations of live, dead and mixed habitats that were constructed using live lodgepole pine seedlings (5 years of age) and surrogate dead trees of similar size. In Chapter 4, I provide a synthesis by outlining the significant findings presented and then suggest silvicultural recommendations to supplement existing management practices. Appendices contain supplemental material, supporting work presented in Chapters 2 and 3. Although the findings presented in the appendices are not robust, stand-alone experiments, they may be useful for future researchers. Appendix A outlines the programming required to reproduce the analyses that interface GIS mapping and statistical modeling of spatial point processes. Details for the construction and use of the "Björklund funnel trap" are outlined in Appendix B. Finally, results of preliminary host choice and no-choice experiments with Warren root collar weevils are presented in Appendix C.

To facilitate the publication of the following work in professional journals, this thesis is written in chapter format. There is some redundancy between chapters, which is necessary to maintain each chapter as a distinct, independent report. Although I am the lead author, the work presented in chapters 2 and 3 is the combined result of a number of authors and hence I will present these sections in the plural voice. We anticipate submitting Chapter 2 to the *Journal of Applied Ecology* and Chapter 3 to *Environmental Entomology* upon thesis completion.

1.1 Literature Cited

Aukema, B. H., A. L. Carroll, J. Zhu, K. F. Raffa, T. A. Sickley, and S. W. Taylor. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. Ecography **29**:427-441.

Byford, G. T. 1994. Warren's root collar weevil in lodgepole pine stands in the Kispiox forest district. MSc. Thesis, University of British Columbia.

Bylund, H., G. Nordlander, and H. Nordenhem. 2004. Feeding and oviposition rates in the pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). Bulletin of Entomological Research **94**:307-317.

Cerezke, H. F. 1970. Method for estimating abundance of weevil, *Hylobius warreni* Wood, and its damage in lodgepole pine stands. Forestry Chronicle **46**:392-396.

Cerezke, H. F. 1973. Survival of the weevil, *Hylobius warreni* Wood, in lodgepole pine stumps. Canadian Journal of Forest Research **3**:367-372.

Cerezke, H. F. 1974. Effects of partial girdling on growth in lodgepole pine with application to damage by the weevil *Hylobius warreni* Wood. Canadian Journal of Forest Research **4**:312-320.

Cerezke, H. F. 1994. Warren rootcollar weevil, *Hylobius warreni* Wood (Coleoptera: Cuculionidae), in Canada: ecology, behaviour, damage relationships, and management. Canadian Entomologist **126**:1383-1442.

Herring, L. J. and H. G. Coates, editors. 1981. Warren's Collar weevil: The underground plantation menace. Province of British Columbia, Ministry of Forests, Prince George, BC.

Hunter, M. D. 2001. Out of sight, out of mind: the impacts of root-feeding insects in natural and managed systems. Agricultural and Forest Entomology **3**:3-9.

Månsson, P. E. and F. Schlyter. 2004. *Hylobius* pine weevils adult host selection and antifeedants: feeding behaviour on host and non-host woody Scandinavian plants. Agricultural and Forest Entomology **6**:165-171.

Matsuoka, S. M., C. M. Handel, and D. R. Ruthrauff. 2001. Densities of breeding birds and changes in vegetation in an Alaskan boreal forest following a massive disturbance by spruce beetles. Canadian Journal of Zoology **79**:1678-1690.

Nordlander, G., H. Nordenhem, and H. Bylund. 1997. Oviposition patterns of the pine weevil *Hylobius abietis*. Entomologia Experimentalis et Applicata **85**:1-9.

Rieske, L. K. and K. F. Raffa. 1990. Dispersal patterns and mark-and-recapture estimates of two pine root weevil species, *Hylobius pales* and *Pachylobius picivorus* (Coleoptera: Curculionidae), in christmas tree plantations. Environmental Entomology **19**:1829-1836.

Rieske, L. K. and K. F. Raffa. 1999. Baited pitfall traps and evaluation of dispensing methods for root weevils (Coleoptera: Curculionidae) in newly established pine plantations in Wisconsin. Journal of Economic Entomology **92**:439-444.

Robert, J. A. and B. S. Lindgren. 2006. Relationships between root form and growth, stability, and mortality in planted versus naturally regenerated lodgepole pine in north-central British Columbia. Canadian Journal of Forest Research **36**:2642-2653.

Schroff, A. Z., B. S. Lindgren, and M. P. Gillingham. 2006. Random acts of weevil: A spatial analysis of *Hylobius warreni* attack on *Pinus contorta* var. *latifolia* in the sub-boreal spruce zone of Northern British Columbia. Forest Ecology and Management **227**:42-49.

Toivonen, R. and H. Viiri. 2006. Adult large pine weevils *Hylobius abietis* feed on silver birch *Betula pendula* even in the presence of conifer seedlings. Agricultural and Forest Entomology **8**:121-128.

Wallertz, K., G. Nordlander, and G. Örlander. 2006. Feeding on roots in the humus layer by adult pine weevil, *Hylobius abietis*. Agricultural and Forest Entomology **8**:1-7.

Werner, R. A., E. H. Holsten, S. M. Matsuoka, and R. E. Burnside. 2006. Spruce beetles and forest ecosystems in south-central Alaska: A review of 30 years of research. Forest Ecology and Management **227**:195-206.

Whitney, R. D. 1961. Root wounds and associated root rots of white spruce. Forestry Chronicle **37**:401-411.

Whitney, R. D. 1962. Studies in forest pathology. Canadian Journal of Botany **40**:1631-1657.

2: LINKS BETWEEN ABOVE- AND BELOW-GROUND HERBIVORY AND CHALLENGES TO FOREST MANAGEMENT: LANDSCAPE-LEVEL IMPACTS OF WARREN ROOT COLLAR WEEVIL FOLLOWING MOUNTAIN PINE BEETLE.

2.1 Abstract

Lodgepole pine, *Pinus contorta* var *latifolia* Dougl. ex. Loud., is a primary component of forests within British Columbia and is vital to the forest industry. An enormous outbreak of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, continues to decimate the pine forests of the province of British Columbia and Alberta, Canada, affecting almost 13 million ha of merchantable forest. Salvage and reforestation efforts are currently underway at landscape-level scales to regenerate affected forests. A concern to these efforts is the migration of a below-ground herbivore, Warren root collar weevil, *Hylobius warreni* Wood, from stands with a reduced host pool, i.e., a high percentage of mature, dead lodgepole pine (>80%), into young, replanted stands, resulting in significant levels of mortality to juvenile trees. The effects of salvage harvesting and replanting following the mountain pine beetle on the development of Warren root collar weevil pressure in young, regenerating stands was examined in lodgepole pine forests in the central interior of British Columbia, Canada. The study was performed in nine stands with trees 9-11 years of age. Gradients of Warren root collar weevil-induced tree mortality were observed at 100-m and entire-cutblock scales. Tree mortality in the cutblocks was highest directly adjacent to the unsalvaged stands, and decreased progressively away from the edge into the cutblock. This gradient of mortality

---

The following chapter is intended for publication with Staffan Lindgren, Michael Gillingham and Brian Aukema as co-authors.

was exacerbated by increasing percentages of pine, more-so if the pine was dead in the mature stand, and the gradient of mortality worsened through time since mountain pine beetle had attacked the adjacent, unsalvaged, mature stands. Weevils attacked the largest trees within the regenerating stands. Gradients of tree mortality caused by Warren root collar weevil suggest significant migration of weevils from adjacent unsalvaged mature stands into regenerating forests. This study reveals a unique link between above-ground and below-ground herbivory in a landscape-level disturbance. Reforestation efforts following salvage harvesting of lodgepole stands with high levels of mountain pine beetle mortality will be complicated by Warren root collar weevil pressure. Management of forests following outbreaks of mountain pine beetle will need to implement silvicultural tools to mitigate potential mortality due to Warren root collar weevils.

2.2 Introduction

Disturbance events play important roles in wide ranges of biotic assemblages and occur at all levels of ecological organization. Insect disturbance agents often have cascading effects on other biological disturbance processes. For example, outbreaks of spruce beetle, *Dendroctonus rufipennis* Kirby, (Coleoptera: Curculionidae: Scolytinae), can cause significant perturbations on forest vegetation and bird populations in the Alaskan boreal forest (Matsuoka et al. 2001). Frequently, above-ground herbivory by insects may affect other above-ground insect herbivores. For example, interspecific competition among the jack pine budworm, *Choristoneura pinus pinus,* (Lepidoptera: Torticidae), and a variety of bark beetles (Coleoptera: Curculionidae: Scolytinae) and woodborers (Coleoptera: Buprestidae and Cerambycidae) can reduce host suitability to future herbivory (Raffa et al. 1998, Wallin and Raffa 2001). Similarly, studies have shown that infestations of western spruce budworm, *Choristoneura occidentalis* Freeman, (Lepidoptera: Tortricidae), in forests of Douglas-fir, *Pseudotsuga menziesii* (Merbel) Franco, increases susceptibility to infestations of Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, (Coleoptera: Curculionidae: Scolytinae) (Negron 1998). Although there are many examples of interactions between above-ground herbivores, we know very little about interactions between below- and above-ground herbivores (Raffa et al. 1998, Blossey and Hunt-Joshi 2003). One potentially important system in which to investigate such relationships includes the above-ground herbivory of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, (Coleoptera: Curculionidae: Scolytinae), and below-ground herbivory of Warren root collar weevil, *Hylobius warreni* Wood, (Coleoptera: Curculionidae) (Warren 1956), a system that also poses significant ecosystem management challenges.

The mountain pine beetle is an eruptive forest insect native to western North America. Over the past few decades, altered disturbance regimes and manifestations of climate change such as increasing winter temperatures (i.e., insufficient to kill substantive proportions of overwintering larvae) have created optimum conditions for outbreaks of this insect (Hicke et al. 2006, Taylor et al. 2006). For example, a current outbreak now extends over almost 13 million ha in British Columbia and north western Alberta, Canada (Westfall and Ebata 2008). Stands of mature lodgepole pine, *Pinus contorta* var *latifolia* Dougl. ex. Loud., the beetle's primary host, have suffered up to 90% mortality in the central interior of British Columbia, where the outbreak first began to erupt (Aukema et al. 2006). Consequently, salvage harvesting operations are underway at unprecedented scales on the landscape of British Columbia, especially in areas where insect populations have exhausted their host supply and collapsed. A significant potential threat to regeneration, however, is the migration of Warren root collar weevils from areas with high percentages of mature, dead, lodgepole pine into nearby, juvenile replantings.

Warren root collar weevils are found throughout the boreal forests of North America. Both males and females are flightless throughout their life cycle. Adult females lay up to 25 eggs a year in the duff layer around the root collar of trees (Cerezke 1994). Upon eclosion, larvae feed on the phloem tissues of the root collar, protected by a hard casing consisting of a mix of frass and tree resin (Cerezke 1970). After 2 years of feeding at the root collar, larvae pupate prior to adult emergence.

Weevils feed on a variety of conifer tree species throughout their development (Hopkins et al. 2008). Adults feed nocturnally on the foliage, descending during dawn hours to rest and/or oviposit. Adult feeding is not detrimental to the host tree, but larval feeding at

the base of young trees may girdle the stems, disrupting translocation, thus inhibiting growth and/or killing the trees. Warren root collar weevils do not feed on dead trees.

Historically, Warren root collar weevil has not been a major forest pest. There are several reasons, however, why this insect may increase ecosystem impacts over the next decade given the massive salvage and replanting efforts that will continue across the affected landscape. First, insects may mature to adults post-harvesting. Following harvesting, larvae and eggs remaining on residual stumps may develop to maturity, yielding a supply of insects to subsequent forests (Cerezke 1973). Larval development may take up to 2 years and adults may live a total of 5 years, resulting in weevil development during the 7 years following the harvesting of stands. Second, larval feeding disproportionately impacts young trees, which will quickly become the predominant age class on the landscape. Recent observations of young stands approximately 4-12 years of age in the central interior of British Columbia have shown cumulative mortality levels as high as 16% (Schroff et al. 2006). Third, reduced host availability (through mortality due to mountain pine beetle) may force weevils to concentrate on remaining live, young trees. This would be especially problematic in situations where unsalvaged, mature stands of predominantly dead pine exist adjacent to planted, regenerating cutblocks containing young trees. Hence, there is great concern that Warren root collar weevils may migrate from areas with high percentages of mature, dead lodgepole pine into regenerating cutblocks, increasing the percentage of young trees killed.

In the present work, we examine the hypothesis that an eruptive above-ground herbivore, the mountain pine beetle, may predispose regenerating stands to increased susceptibility to below-ground herbivory by Warren root collar weevil. We pose 3 questions. First, is there a gradient of mortality from the edge of a mature unsalvaged stand edge into young replantings? If so, what is causing this mortality (i.e., below-ground feeding by larval

Warren root collar weevils)? Second, are potential gradients of mortality mediated by properties of adjacent, unsalvaged stands (e.g., species and live/dead composition, number of years since attack by mountain pine beetle)? Third, do potential spatial patterns of mortality exist only locally, or at scales of entire cutblocks? Answers to these questions, in concert with information on movement patterns and habitat discrimination among labelled weevils (Chapter 3), may provide a foundation to formulate new strategies to limit potential reforestation problems associated with this emerging challenge.

2.3 Materials and Methods

2.3.1 Site Selection

Nine cutblocks were selected across 4 forest districts in the central interior of British Columbia, Canada (Table 2.1). Within each cutblock, trees were of a uniform age. The mean size of each cutblock was 48.75 ± 7.2 ha with a mean stocking density of 3,200 ± 375 stems/ha (means ± SD). Each cutblock had been hand-planted with 95-100% lodgepole pine, at approximately 2- x 2-m spacing, with some evidence of natural regeneration. In some cutblocks, small residual patches of unharvested trees were left to encourage natural regeneration (Sullivan and Sullivan 2001, Sullivan et al. 2001). Logging slash, including stumps from whence immature weevils may develop post-harvesting (Cerezke 1994), had been piled and burned prior to planting. All cutblocks exhibited moderate levels of Warren root collar weevil activity as determined by visual inspection and aerial surveys. Each cutblock was located immediately adjacent to mature stands that were characterized by a high component of mature lodgepole pine recently killed by mountain pine beetle. All sites were found within the sub-boreal spruce (SBS) biogeoclimatic zone (an ecosystem classification

scheme used in British Columbia, Canada (Meidinger and Pojar 1991) and were relatively flat and uniform in composition.

2.3.2 Field Surveys

2.3.2.1 Establishment of transects from perimeter into cutblock

Within each cutblock, up to four, 4-m wide x 100-m long transects were established to identify the presence of gradients of tree mortality radiating into the cutblock from the edge of adjacent, unsalvaged mature stands (Fig. 2.1). Transects were randomly placed around the perimeter of the cutblock. The scale of the transects and plots established at each site was informed by previous research on Warren root collar weevils in young, regenerating stands (Schroff et al. 2006). Along each transect, every tree was measured for vigour (good, moderate, poor and dead), needle chlorosis, height, and spatial location. Tree pathogens such as commandra blister rust, *Cronartium comandrae* Peck, and insects such as spruce gall adelgids, *Adelges cooleyi* Gillette, (Hemiptera: Adelgidae), giant conifer aphids, *Cinara* spp., (Hemiptera: Aphidae), aphid-tending ants including *Camponotus herculeanus* L., (Hymenoptera: Formicidae), northern pitch twig moth, *Petrova albicapitana* Busck, (Lepidoptera: Tortricidae), and terminal weevils, *Pissodes strobi* Peck, (Coleoptera: Curculionidae), were recorded when observed on host coniferous trees (i.e., primarly lodgepole pine and hybrid spruce). However, because their impact was low compared to Warren root collar weevils, their occurrence is not reported. During the summer of 2007, each transect was revisited and any newly deceased trees were identified.

Table 2.1. Summary data for regenerating cutblocks used to study below-ground herbivory by Warren root collar weevil in the central interior of British Columbia, Canada, 2006-2007. Data are provided for 2006. All sites were surrounded by mature, unsalvaged stands of pine, of which the majority of trees had been killed by mountain pine beetle.

Cutblock	Forest District	Stocking Density (stems/ha)	Composition[a]	Age[b]	Latitude	Longitude	Size (ha)	Residual Harvest Patches
A	Quesnel	2000	Pine	10	53 18' 12"	123° 38' 30"	56.2	No
B	Quesnel	2362	Pine	8	53 23' 45"	123° 08' 55"	39.5	No
C	Prince George	3500	Pine	11	54 15' 13"	122° 46' 32"	84.9	No
D	Vanderhoof	5381	Pine	9	53 33' 03"	125° 05' 22"	41.9	No
E	Nadina	4612	Pine	9	53 29' 49"	125° 18' 00"	39.0	Yes
F	Nadina	2675	Pine	10	53 32' 41"	125° 23' 09"	73.0	Yes
G	Vanderhoof	3250	Pine	9	53 50' 34"	123° 37' 47"	47.2	No
H	Vanderhoof	2587	Pine	8	53 51' 19"	123° 32' 33"	41.6	Yes
I	Vanderhoof	2412	Pine	10	53 30' 59"	124° 33' 32"	15.5	Yes

[a]All stands were either planted with 95-100% lodgepole pine
[b]Small portions of some cutblocks had been replanted post-planting

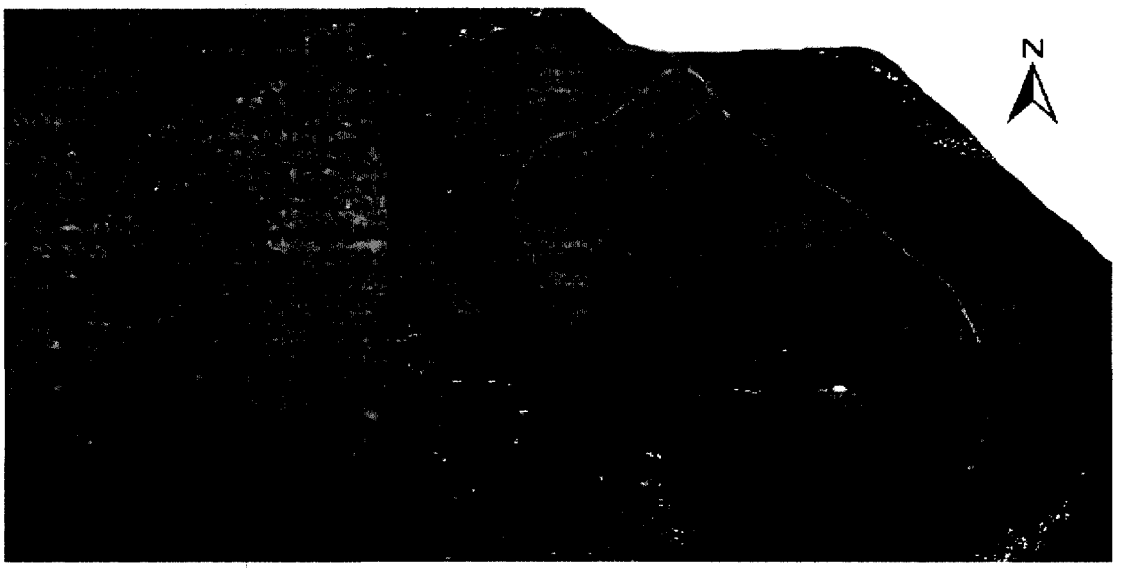


Figure 2.1. Diagrammatic representation of the layout of transect (line) intensive sampling plots (boxes) and stand characterization plots (circles). White along cutblock edges is snow (Photo taken 05/14/2007).

2.3.2.2 Intensively-sampled plots within cutblock

Transects provide useful information on the location of dead trees, but not necessarily the causative agents of mortality. Injury by larvae of Warren root collar weevils, for example, can only be determined by careful excavation of the soil around the root collar of young trees and examination of feeding scars, girdling, and/or sap casings. Therefore, 8- x 8-m plots were installed for intensive sampling at 0-, 50- and 100-m marks along each transect to determine whether mortality was correlated with weevil injury (Fig. 2.1). Feeding was evaluated on all trees within each plot by looking for sap casings and/or the presence of larvae at the root collar (Cerezke 1994). Dead trees were recorded as killed by Warren root collar weevil if girdling was observed. Trees were also measured for vigour, height, spatial location, length of terminal growth from previous year, length of terminal growth from 2 years previous, ground-level diameter, and diameter at breast height. Similar to trees along

the transect, trees within the intensive sampling plots were also examined for other insect pests and fungal pathogens but findings are not presented due to low incidences. Each 8- x 8-m intensive sampling plot was re-sampled the summer of 2007 to record any changes in tree mortality and larval feeding by Warren root collar weevil.

2.3.2.3 Characterization of stands killed by mountain pine beetle

Perpendicular to each transect, 3 circular plots 15 m in diameter were established in the mature, unsalvaged stands killed by mountain pine beetle (Fig. 2.1). The centre of the first plot was located 15 m from the stand edge and the beginning of the 100-m transect. The second and third plots were located 25 m on either side of the centre of the first plot, also 15 m from the stand edge (Fig. 2.1). Plot boundaries were established using a BAF #4 prism (Cruise Master Prisms INC. Sublimity, OR, USA). Trees within each plot were cencused for species, diameter at breast height, evidence of mountain pine beetle attack (never attacked, colonized, post-colonized, and dead), and time since mountain pine beetle attack. Time since mountain pine beetle attack was estimated using the characteristics of the attacked tree including brood (if present), the amount of bark left on the tree, the colouration of needles, and the amount of needles left in the crown. Where there was evidence of attack over several years, we assigned the stand a value of the average estimated attack date of all trees surveyed in the plot. Because visual estimation methods are subjective (Safranyik et al. 1974, Shore and Safranyik 1992), especially where trees are killed rapidly by extremely high densities of mountain pine beetle, we compared estimates of attack against aerial survey records of mountain pine beetle attack (Aukema et al. 2006). Visual dating methods were highly consistent with these spatial records (Klingenberg, unpublished data).

2.3.2.4 Statistical analysis

Generalized linear mixed effects models were used to examine the fixed effects of variables characterizing individual tree measurements within the cutblock along the transect (i.e., tree heights, vigour (dead, poor, moderate, or good, fit as four separate 0/1 indicator variables, etc.), the trees' spatial positions (i.e., distances from stand edges), and mensurational data from the mature stands adjacent to the cutblocks on binary response variables. These response variables included tree status (live/dead), and presence/absence of feeding scars at the root collar of host trees. For the latter response, analysis was restricted to data from the intensively sampled plots. Random effects included site and transect nested within site, as sites and transects within the sites were selected at random from all potentially suitable areas with the central interior of British Columbia. Models were constructed using a stepwise, backwards elimination procedure from full models to determine which predictor variables to retain using $\alpha = 0.05$. Because various stepwise model selection techniques may result in different final models, frequently due to the presence of collinearity among variables (e.g., Aukema et al. 2005), various backwards elimination strategies were investigated, especially where correlations were suspected (e.g., between dependent variables such as tree height and diameter). Model space always converged to a unique, simple, parsimonious model, however. Model selection was not performed using automated techniques.

Separate regressions were developed for data collected in 2006 and 2007. For example, in 2007, logistic regression with newly attacked trees in 2007 as the response variable was used to test the effects of tree vigour in 2006 on the probability of a tree being dead in 2007. All data analysis was performed in R v.2.5.0 (Ihaka and Gentleman 1996; R Development Core Team 2008).

2.3.3 Aerial Surveys

2.3.3.1 Patterns of mortality within entire cutblocks

Although gradients of tree mortality from stand edges into the cutblocks might infer migration of Warren root collar weevils into the plots from neighbouring mature stands with reduced host availability, we were concerned that focusing solely on edge effects might miss important patterns of mortality within the cutblocks such as clusters or "hotspots", implying endemic increases of resident weevils developing from stumps left from logging slash (Cerezke 1994). Patterns of tree mortality may be caused by multiple, and often interacting, mechanisms (Aukema et al. 2006). We used aerial photographs of each of the 9 cutblocks where transects and intensive plots were located. Photographs (6496 x 4872 pixels, at an average ground sampling distance (GSD) of 20-cm/pixel) were taken of each cutblock using an Imacon Ixpress 132C 22 megapixel camera with an 80-mm lens (Rodenstock Apo-Sironar digital HR Lens with a Rollei Electronic Shutter). In instances where a single photo could not capture an entire cutblock, photos were merged using Adobe Photoshop v.9.0.2 (Adobe, San Jose, California). All photos were then imported into Arcview v.9.2 (ESRI, Redlands, California), where each young tree that had died over the past year (i.e., visibly red) was spatially referenced.

2.3.3.2 Statistical analysis

The x and y coordinates for each dead tree were exported from Arcview and imported into R v.2.5.0 for point pattern analysis of each cutblock (spatstat package v.1.12-6). We fit spatial point process models of the intensity of dead trees, λ (in trees/m^2), within each cutblock. Null models contained only an intercept, signifying constant intensity, or a homogenous Poisson process assuming complete spatial randomness. Further models explored x and y covariates (i.e., a gradient of mortality in either east-west or north-south

direction(s)), and a distance covariate measuring distance from any point in the cutblock to the nearest residual stand (usually plot edge). Significance of these spatial covariates indicated an inhomogenous Poisson point process, i.e., the presence of (a) gradient(s) of mortality of dead trees at the level of the entire cutblock. Nested models were compared using likelihood ratio tests against a χ^2 reference distribution to select the best model, because the likelihoods of these models are well defined (Berman and Turner 1992).

2.4 Results

2.4.1 Field Surveys

2.4.1.1 Intensively sampled plots

Overall, we found that trees with feeding scars had a 17% probability of dying in a given year (Table 2.2). Within the intensively sampled plots the annual mortality rate was 3%, judged by trees that had recently died and retained red needles. Of these 38 dead trees, 87% exhibited partial or complete girdling by larvae of Warren root collar weevil. Seventeen per cent of the trees surveyed exhibited evidence of larval feeding by Warren root collar weevil.

Larval feeding activity decreased with distance from the mature unsalvaged stand. At the same time, feeding activity increased with tree diameter at ground level. After correcting for tree size we also found feeding activity increased if the tree was planted vs. regenerating naturally (Table 2.2). Indeed, weevils appeared to preferentially feed on the most dominant young trees in the cutblock, as analysis of the data collected in the intensively sampled plots in 2007 indicated that tree height was positively correlated with trees having new feeding scars (Table 2.2).

Table 2.2. Regression models predicting tree mortality and Warren root collar weevil feeding scars of young lodgepole pine trees within cutblocks in the central interior of British Columbia. Coefficient estimates are provided on the first line for each model, with standard errors of the estimates provided below on the second line in parentheses. All variables listed are significant using $\alpha = 0.05$. All models also include random effects of site and transect nested within site.

Model	Data set[a]	Year of sampling	Response variable[b]	Intercept	Larval feeding	Transect distance	Natural / planted (0/1)	Ground Level Diameter	Tree height	Moderate vigour (0/1)	Poor vigour (0/1)	% pine[c]	% dead pine[c]	Time since death[c]	*n* trees
A	Full	2006	Tree mortality	-3.66		-0.0078			0.0072						2,565
				(0.35)		(0.0037)			(0.0018)						
B	Full	2007	Tree mortality	-5.54					0.012	2.12	2.77				2,565
				(0.37)					(0.0026)	(0.51)	(0.53)				
C	Full	2006	Tree mortality	-8.32		-0.0078			0.0071			0.04	0.025	0.64	2.565
				(1.04)		(0.0037)			(0.0018)			(0.081)	(0.012)	(0.20)	
D	Reduced	2006	Tree mortality	-5.28	3.69										1,117
				(0.47)	(0.50)										
E	Reduced	2006	Larval feeding	-3.83		-0.0076	0.97	0.069							685
				(0.42)		(0.0031)	(0.29)	(0.0011)							
F	Reduced	2007	Larval feeding	4.68					0.0097						918
				(0.44)					(0.0022)						

[a]The full data set includes the data collected from all trees along the 100-m transects; the reduced data set is restricted to trees sampled within the 8 x 8-m intensively sampled plots

[b]The binary, yes / no response variables of tree mortality and larval feeding may be back transformed using $\exp(y)/(1 + \exp(y))$ to obtain the probability of a tree being dead or exhibiting feeding scars

[c]These variables were recorded from the mature unsalvaged stand adjacent to transects and plots established within cutblocks

2.4.1.2 Associations of mortality observed in transects with characteristics of neighbouring, unsalvaged stands.

Along each transect, we observed, on average, 5% mortality. Mortality decreased with increasing distance away from the adjacent unsalvaged mature stand, and larger trees were more likely to be found dead (Model A in Table 2.2). Trees within each cutblock appeared to be spatially uniform in size, as there was no statistical relationship between tree height and distance along the transect away from the adjacent unsalvaged mature stand edge. The positive relationship between tree size and likelihood of death persisted across both years, as analysis of the data collected the second summer revealed that the probability of a tree's death along each transect was positively correlated with the trees height and condition the previous year (Model B in Table 2.2).

On average, the mature stands were approximately 90% pine, and of these trees, between 70 and 80% were dead. Stands had been attacked by mountain pine beetle 0-5 years prior to sampling. Statistical associations between tree mortality within the regenerating cutblocks, distance from the stand edge, and individual tree height remained consistent when these data on the neighbouring, mature, unsalvaged stands were included in model building. Not only were relationships among tree mortality, distance from stand edge, and tree height consistent with previous regression models, but these variables helped explain additional mortality observed within the regenerating cutblocks. Tree mortality of young trees along each transect increased with increasing pine composition, increasing mortality within the stand, and the number of years since mountain pine beetle attack in the unsalvaged mature stands adjacent to each transect (Model C in Table 2.2).

It is possible that the higher number of dead trees observed along cutblock margins was simply an artefact of a higher density of trees there, e.g., due to natural ingress. Natural

regeneration was observed along the transects and within the intensively sampled plots, which is characteristic of lodgepole pine forests in the central interior of British Columbia (Burton 2002). To preclude the possibility that higher tree densities along stand edges might in fact be creating conditions of constant relative mortality, we conducted a regression comparing tree density with distance from the mature stand edge. No significant gradients of tree density were observed within any of the 9 cutblocks censused ($P > 0.05$), indicating that gradients of mortality were not statistical artefacts of tree density.

2.4.2 Aerial Surveys

2.4.2.1 Patterns of mortality within entire cutblocks

We identified between 200 and 5000 dead trees in each of the 9 cutblocks from the high resolution aerial photographs. All dead trees were identified by the presence of red, necrotic needles, indicating that they had died within the past year. Locations of the dead trees and the observed density surface of a representative cutblock are displayed in Fig. 2.2. (Supplemental density and distance to margin surfaces for all cutblocks are displayed in Appendix A). Graphically, it appears that there is a higher intensity or density of dead trees along the edges of the cutblock (adjacent to unsalvaged, mature stands of dead lodgepole pine). Regression models of the intensity of dead trees, λ (i.e., number of dead trees/m^2), as a function of either a constant intercept (i.e., a homogenous Poisson process), or as a function of spatial covariates (i.e., gradient(s) in any of a number of directions or from stand edges, signifying inhomogeneous Poisson processes), are summarized for each of the cutblocks in Table 2.3.

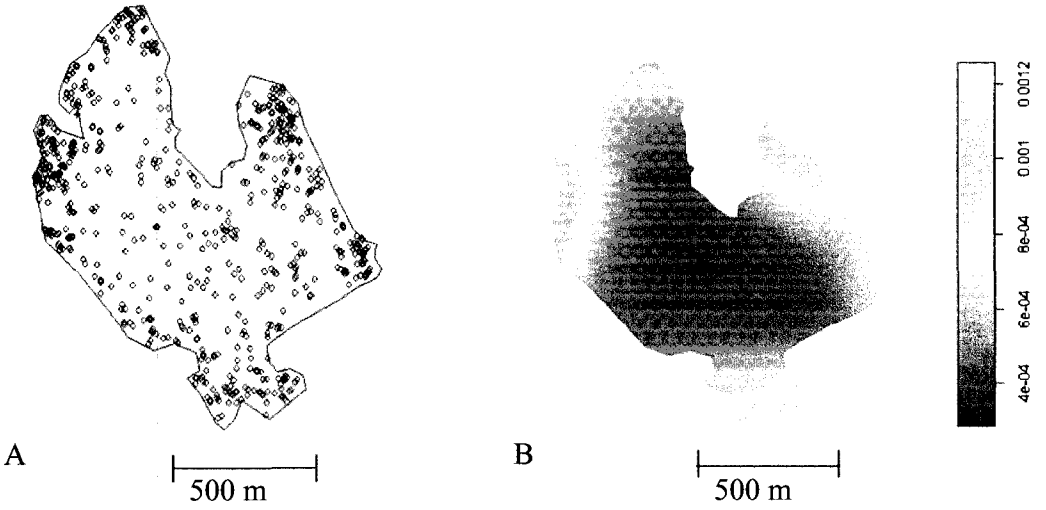


Figure 2.2. Plot of (A) spatial location of dead trees, and (B) intensity surface of a representative cutblock (cutblock D in Table 2.1). Units for plot B are dead trees per meter squared.

Within 6 of the 9 cutblocks (B, C, D, E, F and G), the intensity of mortality was found to be greatest directly adjacent to all unsalvaged mature stand edges, and to gradually decrease with distance to edge into the cutblock. One cutblock was observed to have directional gradients of mortality in the y and x directions (I), while another was observed to only have a gradient in the y direction (H). One cutblock was observed to have a significant gradient of mortality from the centre of the cutblock to the edges in a north/south direction (A).

Table 2.3. Best models for modeling the intensity of dead trees per m^2 in 9 cutblocks in the central interior of British Columbia, Canada. Coefficient estimates are provided on log-linear scale. For example, for cutblock B, $\log(\lambda) = -4.46 - 4.70\text{x}10^{-04}$ (*distance in x direction*) $- 2.20\text{x}10^{-03}$(*distance to margin*). Covariates x and y account for potential linear trends. The covariate measuring *distance to margin* accounts for potential quadratic trends in x and y, so these are not fit unless the *distance to margin* effect is not significant.

Cutblock	*Intercept*		*Distance to margin*		*Distance in X direction*		*Distance in Y direction*		Model fit (vs. null)[a]			λ^b	Intensity gradient[c]
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Chisq	Df	*P*		
A	-6.26	$2.90\text{x}10^{-02}$										18.55	none[d]
B	-4.46	$4.06\text{x}10^{-02}$	$-2.20\text{x}10^{-03}$	$3.04\text{x}10^{-04}$			$-4.70\text{x}10^{-04}$	$5.12\text{x}10^{-05}$	162.70	22	<0.001	70.93	uni-directional & from all edges
C	-9.98	$36.0\text{x}10^{-02}$	$-5.10\text{x}10^{-04}$	$1.40\text{x}10^{-03}$	$-1.00\text{x}10^{-03}$	$2.70\text{x}10^{-04}$	$3.60\text{x}10^{-03}$	$5.90\text{x}10^{-04}$	1022.20	3	<0.001	3.75	bi-directional & from all edges
D	-6.76	$6.10\text{x}10^{-02}$	$-7.00\text{x}10^{-03}$	$6.10\text{x}10^{-04}$					154.30	1	<0.001	5.96	from all edges
E	-5.09	$7.60\text{x}10^{-02}$	$-2.20\text{x}10^{-03}$	$7.80\text{x}10^{-04}$	$-8.00\text{x}10^{-04}$	$1.70\text{x}10^{-04}$	$-5.70\text{x}10^{-04}$	$1.30\text{x}10^{-04}$	38.80	3	<0.001	58.24	bi-directional & from all edges
F	-6.23	$4.67\text{x}10^{-02}$	$-7.80\text{x}10^{-04}$	$2.72\text{x}10^{-04}$	$-3.90\text{x}10^{-04}$	$2.16\text{x}10^{-05}$	$3.00\text{x}10^{-04}$	$4.88\text{x}10^{-05}$	493.80	3	<0.001	38.30	bi-directional & from all edges
G	-9.11	$2.18\text{x}10^{-01}$	$-1.90\text{x}10^{-03}$	$5.80\text{x}10^{-04}$	$1.80\text{x}10^{-04}$	$5.34\text{x}10^{-05}$	$1.20\text{x}10^{-03}$	$1.35\text{x}10^{-04}$	98.33	3	<0.001	2.25	bi-directional & from all edges
H	-6.38	$17.00\text{x}10^{-02}$			$8.00\text{x}10^{-04}$	$8.00\text{x}10^{-04}$			78.99	1	<0.001	3.50	uni-directional
I	-6.75	$1.54\text{x}10^{-01}$			$-1.10\text{x}10^{-03}$	$8.45\text{x}10^{-05}$	$-1.20\text{x}10^{-03}$	$1.91\text{x}10^{-04}$	247.10	2	<0.001	16.40	bi-directional

[a]Null model contains only the intercept (a homogenous Poisson process, constant intensity with no gradient)

[b]Intensiy of mortality for the null model of each cutblock (dead trees/ha)

[c]Judged by sign and significance of terms for x and/or y (uni-/bi-directional) and/or *distance to margin* (gradient from all edges), in the final model

[d]Quadratic gradient in north-south direction was evident with highest intensity in centre of cutblock; $\log(\lambda) = -7.07(\pm 0.14) - 2.98\text{x}10^{-03}(\pm 5.04\text{x}10^{-04})$(*distance in y direction*) $- 2.25\text{x}10^{-06}(\pm 4.27\text{x}10^{-07})$(*distance in y direction*)^2

2.5 Discussion

Our results provide evidence that the current landscape-level outbreak of mountain pine beetle in the central interior of British Columbia, Canada will have direct consequences for reforestation due to below-ground herbivory by Warren root collar weevil within young, replanted stands. Our findings that Warren root collar weevil-induced mortality was positively associated with the level of pine composition and mortality in adjacent mature stands as well as with time since mountain pine beetle had attacked stands are consistent with the hypothesis that Warren root collar weevils are migrating out of mature, unsalvaged stands into young regenerating stands in search of food. Two other lines of evidence support this hypothesis. First, weevils do not feed on dead trees (Cerezke 1994). Second, these insects are able to discriminate between habitat types and exhibit increased movement rates in habitats with a high component of dead vs. live trees (Chapter 3).

Warren root collar weevil feeding induced-tree mortality may continue to be an elevated concern as the outbreak of mountain pine beetle declines and forests are consequently salvaged and replanted. Because lodgepole pine is a primary component of regenerating stands and also a primary host of Warren root collar weevils (Cerezke 1994), the negative effects of this insect will occur at the landscape scale. As more trees within the mature unsalvaged stands are killed by mountain pine beetle, weevils will likely continue to migrate into adjacent cutblocks. Warren root collar weevils appeared to preferentially attack the largest, and presumably healthiest, replanted trees, even after accounting for the effects of mortality gradients from stand margins. Although Warren root collar weevil may only kill a percentage of young trees, larval feeding on the root collar will decrease stand productivity

(Cerezke 1994). Larval feeding causes trees to lose vigour. Trees that were moderate or poor in vigour one year were likely to be dead the following year.

Warren root collar weevil migration from mature unsalvaged stands into young regenerating stands following outbreaks of mountain pine beetle can be justified within the context of insect dispersal patterns. Local habitat conditions are known to affect the patterns of insect dispersal (Haynes and Cronin 2003, Haynes et al. 2007), specifically in relation to habitat conditions created following clear-cut harvesting (Bengtsson et al. 1997, Niemelä et al. 1993). Previous studies have shown that Warren root collar weevil movement is modified by the presence of dead or live host trees (Chapter 3). This elevated movement observed in low-quality habitats containing dead trees helps explain the migration of weevils into young lodgepole pine replantings following the recent outbreak of mountain pine beetle.

We found that weevils selected trees that were planted over trees that were naturally seeded from adjacent stands. Because planted trees have been found to have a smaller cross-sectional area, they are thought to be at a higher risk of mortality from larval girdling (Robert and Lindgren 2006). Hence, in addition to migration effects, apparent preference by weevils for planted trees may explain why levels of mortality are elevated in young plantations. Encouraging natural regeneration and improving planting practices of lodgepole pine seedings to reduce "J-root" may increase the health of trees and reduce the risk of mortality due to these insects (Duke and Lindgren 2006, Robert and Lindgren 2006). Larval feeding also opens infection corridors for fungal pathogens that increases the annual chance of mortality (Whitney 1961, 1962).

Patterns of tree mortality found at the 100-m transect and intensively sampled scales were found to be consistent with our examination of mortality patterns of entire cutblocks. Our findings suggest that 6 cutblocks exhibited gradients of mortality into the cutblocks

around the entire perimeter of each cutblock, which is in accordance with findings at the transect and intensive sampling plot scales (Table 2.3). Two cutblocks were observed to have gradients of mortality, but they were not found to be consistently associated with all margins into the cutblocks. One cutblock was found to have a gradient of mortality that decreased toward margins. Such patterns may be due, in part, to the retention of residual patches of mature, dead pine within the cutblocks. For example, one of the cutblocks (I) without significant gradients from all edges was observed to contain eight residual patches of mature lodgepole pine to serve as wildlife habitat. Not surprisingly, this pine had also been recently killed by mountain pine beetle. These residual patches may obfuscate gradients of young tree mortality from margins, as weevils may create internal opposing gradients by migrating from these residual patches.

Although above-ground herbivory by mountain pine beetle may trigger large-scale movement by Warren root collar weevil due to declining host availability, mountain pine beetle may indirectly benefit Warren root collar weevils by creating site conditions that favour insect development. There are two potentially important examples of this. First, the suddenly reduced transpiration potential due to mountain pine beetle killing large tracts of mature forest has elevated the water table in many areas. Warren root collar weevils prefer moist habitats (Cerezke 1994). Two cutblocks without significant gradients from all edges (H and A) displayed mortality concentrated within areas of the cutblock thought to have higher soil moistures. Second, anthropogenic remediation efforts may inadvertently create site conditions that are beneficial to weevil populations. Habitat modification associated with clear-cut harvesting affects a variety of aspects of forest ecology, including insect communities (Niemelä et al. 1993, Bengtsson et al. 1997, Heliölä et al. 2001, Lemieux and Lindgren 2004, Latty et al. 2006), and forest-management practices mediate the dispersal

patterns and population dynamics of other *Hylobius* species (Eidmann 1997, Leather et al. 1999, Rieske and Raffa 1999, Nordlander et al. 2003, Nordlander et al. 2005). For example, Warren root collar weevils benefit from increased duff layer, that may exist following clear-cut harvesting, especially if slash is not burned prior to replanting (Cerezke, 1994).

High risk areas of Warren root collar weevil infestation can be identified by characterizing the condition of adjacent mature stands. Warren root collar weevil induced tree mortality within young regenerating stands is correlated with levels of mountain pine beetle infestation of neighbouring mature stands; therefore, caution should be taken when replanting trees adjacent to mature lodgepole pine forests that have been attacked by mountain pine beetle. Warren root collar weevil migration into young regenerating stands may be complicated by current reforestation practices in British Columbia. Current harvesting and reforestation practices attempt to mimic historic fire regimes (Bergeron et al. 2002) and encourage the implementation of smaller cutblocks (DeLong 2002), which are often replanted with high percentages of pine trees susceptible to Warren root collar weevil (Cerezke 1994, Hopkins et al. 2008). Smaller cutblocks with a high percentage of susceptible hosts may be prone to greater concentration of weevil populations, resulting in elevated mortality levels. Potential forest management strategies that could ameliorate impacts of Warren root collar weevil could include: (a) identifying sites prone to Warren root collar weevil related forest health issues, (b) implementing post-harvest techniques (i.e., prescribed burning and scarification) to remove excess slash and stumps that favour the development of populations of Warren root collar weevil remaining in stands, (c) incorporating less susceptible host tree species (i.e., *Abies*, *Picea, Larix*, *Pseudotsuga* spp, or any deciduous species) into prescribed planting mixes, (d) maintaining high stocking standards and limiting pre-commercial thinning treatments to maintain conditions less

favourable to Warren root collar weevil development. Any such strategies, however, must be undertaken with input from multiple stakeholders involved. Our finding that Warren root collar weevil pressure is connected to the extent of mountain pine beetle infestation of nearby stands will be useful when implementing forest management practices (Cerezke 1994) to reduce tree mortality of regenerating stands.

2.6 Acknowledgements

We thank Ken White and Carolyn Stevens from the British Columbia Ministry of Forests and Range for their help with site selection. We thank the "LAPH" forest entomology research cluster (Laboratories of B.S. Lindgren, B.H. Aukema, L. Poirier and D. Huber) at the University of Northern British Columbia for valuable input and discussion at all stages of research. Industrial Forest Service, Prince George, British Columbia, provided the aerial photographs. Thanks to Sandy Allen, Hollie Moore, Talya Truant, and Gareth Hopkins for help collecting field data. The study was financially supported by a British Columbia Forest Science Program project M086046, the Canadian Forest Service, and Pacific Forestry Centre Graduate and UNBC Graduate awards to MDK.

2.7 Literature Cited

Aukema, B. H., A. L. Carroll, J. Zhu, K. F. Raffa, T. A. Sickley, and S. W. Taylor. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. Ecography **29**:427-441.

Aukema, B. H., M. K. Clayton, and K. F. Raffa. 2005. Modeling flight activity and population dynamics of the pine engraver, Ips pini, in the Great Lakes region: effects of weather and predators over short time scales. Population Ecology **47**:61-69.

Bengtsson, J., T. Persson, and H. Lundkvist. 1997. Long-term effects of logging residue addition and removal on macroarthropods and enchytraeids. Journal of Applied Ecology **34**:1014-1022.

Bergeron, Y., A. Leduc, B. D. Harvey, and S. Gauthier. 2002. Natural fire regime: A guide for sustainable management of the Canadian boreal forest. Silva Fennica **36**:81-95.

Berman, M. and T. R. Turner. 1992. Approximating point process likelihoods with GLIM. Applied Statistics **41**:31-38.

Blossey, B. and T. R. Hunt-Joshi. 2003. Belowground herbivory by insects: Influence on plants and aboveground herbivores. Annual Review of Entomology **48**:521-547.

Burton, P. J. 2002. Effects of clearcut edges on trees in the sub-boreal spruce zone of NorthIst-Central British Columbia. Silva Fennica **36**:329-352.

Cerezke, H. F. 1970. Method for estimating abundance of weevil, *Hylobius warreni* Wood, and its damage in lodgepole pine stands. Forestry Chronicle **46**:392-396.

Cerezke, H. F. 1994. Warren rootcollar weevil, *Hylobius warreni* Wood (Coleoptera: Cuculionidae), in Canada: ecology, behaviour, damage relationships, and management. Canadian Entomologist **126**:1383-1442.

DeLong, S. C. 2002. Using nature's template to best advantage in the Canadian boreal forest. Silva Fennica **36**:401-408.

Duke, L. and B. S. Lindgren. 2006. Attack by *Hylobius warreni* on grafted lodgepole pine and its relationship with monoterpene composition and scion: rootstock diameter ratio. Agricultural and Forest Entomology **8**:305-311.

Eidmann, H. H. 1997. Assessment of pine weevil numbers on clear-cut and forest sites with shelter boards and pitfall traps. Anzeiger Fur Schadlingskunde Pflanzenschutz Umlltschutz **70**:68-72.

ESRI. 2008. GIS and mapping software. 380 New York Street, Redlands, CA 92373-8100

Haynes, K. J. and J. T. Cronin. 2003. Matrix composition affects the spatial ecology of a prairie planthopper. Ecology **84**:2856-2866.

Haynes, K. J. and J. T. Cronin. 2006. Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. Oikos **113**:43-54.

Haynes, K. J., F. P. Dillemuth, B. J. Anderson, A. S. Hakes, H. B. Jackson, S. E. Jackson, and J. T. Cronin. 2007. Landscape context outweighs local habitat quality in its effects on herbivore dispersal and distribution. Oecologia **151**:431-441.

Heliölä, J., M. Koivula, and J. Niemelä. 2001. Distribution of Carabid beetles (Coleoptera: Carabidae) across a boreal forest-clearcut ecotone. Conservation Biology **15**:370-377.

Hicke, J. A., J. A. Logan, J. Polll, and D. S. Ojima. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. Journal of Geophysical Research-Biogeosciences **111**., G02019, doi:02010.01029/02005JG000101

Hopkins, G. R., M. D. Klingenberg, and B. H. Aukema. 2008. Feeding and ovipositional behaviour of *Hylobius warreni* Wood (Coleoptera: Curculionidae) on host and non-host bark in laboratory bioassays. Agricultural and Forest Entomology: Accepted pending revisions.

Ihaka, I. and R. Gentleman. 1996. R: a language for data analysis and graphics. Journal of Computational Graphical Statistics **5**:299-314.

Latty, E. F., S. M. Irner, D. J. Mladenoff, K. F. Raffa, and T. A. Sickley. 2006. Response of ground beetle (Carabidae) assemblages to logging history in northern hardwood-hemlock forests. Forest Ecology and Management **222**:335-347.

Leather, S. R., K. R. Day, and A. N. Salisbury. 1999. The biology and ecology of the large pine weevil, *Hylobius abietis* (Coleoptera : Curculionidae): a problem of dispersal? Bulletin of Entomological Research **89**:3-16.

Lemieux, J. P. and B. S. Lindgren. 2004. Ground beetle responses to patch retention harvesting in high elevation forests of British Columbia. Ecography **27**:557-566.

Matsuoka, S. M., C. M. Handel, and D. R. Ruthrauff. 2001. Densities of breeding birds and changes in vegetation in an Alaskan boreal forest following a massive disturbance by spruce beetles. Canadian Journal of Zoology **79**:1678-1690.

Meidinger, D. and J. Pojar. 1991. Ecosystems of British Columbia, Special Report Series 6. BC Ministry of Forests Victoria, BC.

Negron, J. F. 1998. Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. Forest Ecology and Management **107**:71-85.

Niemelä, J., D. Langor, and J. R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conservation Biology **7**:551-561.

Nordlander, G., H. Bylund, and N. Björklund. 2005. Soil type and microtopography influencing feeding above and below ground by the pine weevil *Hylobius abietis*. Agricultural and Forest Entomology **7**:107-113.

Nordlander, G., H. Bylund, G. Örlander, and K. Wallertz. 2003. Pine weevil population density and damage to coniferous seedlings in a regeneration area with and without shelterwood. Scandinavian Journal of Forest Research **18**:438-448.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org.

Raffa, K. F., S. C. Krause, and P. B. Reich. 1998. Long-term effects of defoliation on red pine suitability to insects feeding on diverse plant tissues. Ecology **79**:2352-2364.

Rieske, L. K. and K. F. Raffa. 1999. Baited pitfall traps and evaluation of dispensing methods for root weevils (Coleoptera: Curculionidae) in newly established pine plantations in Wisconsin. Journal of Economic Entomology **92**:439-444.

Robert, J. A. and B. S. Lindgren. 2006. Relationships between root form and growth, stability, and mortality in planted versus naturally regenerated lodgepole pine in north-central British Columbia. Canadian Journal of Forest Research **36**:2642-2653.

Safranyik, L., D. M. Shrimpton, and H. S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Forestry Technical Report 1, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia **1**:1-23.

Schroff, A. Z., B. S. Lindgren, and M. P. Gillingham. 2006. Random acts of weevil: A spatial analysis of *Hylobius warreni* attack on *Pinus contorta* var. *latifolia* in the sub-boreal spruce zone of Northern British Columbia. Forest Ecology and Management **227**:42-49.

Shore, T. L. and L. Safranyik. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Forestry Canada, Pacific and Yukon Region, Pacific Forestry Centre, Victoria British Columbia:1-12.

Sullivan, T. P. and D. S. Sullivan. 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. Journal of Applied Ecology **38**:1234-1252.

Sullivan, T. P., D. S. Sullivan, and P. M. F. Lindgren. 2001. Influence of variable retention harvests on forest ecosystems. I. Diversity of stand structure. Journal of Applied Ecology **38**:1221-1233.

Taylor, S. W., A. L. Carroll, R. I. Alfaro, and L. Safranyik. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia.

Wallin, K. F. and K. F. Raffa. 2001. Effects of folivory on subcortical plant defenses: Can defense theories predict interguild processes? Ecology **82**:1387-1400.

Warren, G. L. 1956. Root Injury to conifers in Canada by species of *Hylobius* and *Hypomolyx* (Coleoptera: Curculionidae). Forestry Chronicle **32**:7-10.

Westfall, J. and T. Ebata. 2008. 2007 Summary of forest health conditions in British Columbia. Pest Management Report Number 15. BC Ministry of Forests and Range, Victoria, BC.

Whitney, R. D. 1961. Root wounds and associated root rots of white spruce. Forestry Chronicle **37**:401-411.

Whitney, R. D. 1962. Studies in forest pathology. Canadian Journal of Botany **40**:1631-1657.

3: DIFFERENTIAL DISPERSION OF WARREN ROOT COLLAR WEEVIL (*Hylobius warreni* Wood) WITHIN MODIFIED FOREST HABITATS.

3.1 Abstract

Warren root collar weevil (*Hylobius warreni* Wood) is a flightless insect that feeds on conifers throughout the boreal forests of Canada. Mature trees typically are not killed by this insect, but larval feeding at the root collar may injure and kill young trees. Recently, a large outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has killed up to 80% of the mature lodgepole pine in British Columbia, Canada, leading to a hypothesis that adult weevils may migrate from these mature forests with reduced host pools into young, salvaged and replanted forests when the two habitat types are located adjacent to each other. Little is known about movement of these walking weevils in different habitat types, however. During the spring of 2007, we constructed three research plots consisting of various combinations of live tree, dead tree and mixed (i.e., live and dead) tree habitats. We observed dispersal patterns of labelled insects over a 28 day period using a novel insect trap attached to the base of trees. Approximately 35% of the Warren root collar weevils were recaptured. Weevils were more likely to be captured close to the release location in the mixed and live habitats, vs. dead habitats. Weevils dispersed quickly when released in the middle of the plot with dead trees, moving at a rate of 1.2 m/day, almost double the rates of insects released in live and mixed habitats. Our findings provide evidence that Warren root collar weevils may disperse out of habitats with higher proportions of dead trees into habitats with higher

---

The following chapter is intended for publication with Niklas Björklund and Brian Aukema as co-authors.

proportions of live trees. This is a potentially worrisome finding, given the current landscape-scale modification of lodgepole pine forests in western Canada by outbreaks of mountain pine beetle. Our results are discussed in the context of habitat discrimination and reforestation efforts following the recent mountain pine beetle infestation in British Columbia.

3.2 Introduction

Elucidating processes that contribute to spatial patterns of the dispersal of insect herbivores is a challenge, as dispersal may depend on multiple and interacting factors including the physiological status of the insects (e.g., reproductive status, energy reserves) and population density (e.g., migration, crowding). Habitat conditions, such as composition and quality of the habitat matrix or patches may also affect insect dispersal (Haynes and Cronin 2003, Nathan et al. 2003, Haynes and Cronin 2006). For example, within boreal forest ecosystems, habitat alterations such as clear-cut harvesting can affect the spatial distribution of insect assemblages (Niemelä et al. 1993, Bengtsson et al. 1997, Heliölä et al. 2001, Lemieux and Lindgren 2004, Phillips et al. 2006). Species perturbations in forested environments are not limited to anthropogenic impacts. For example, insect disturbances may affect the spatial or temporal dynamics of other insects as well (Denno et al. 1995). Currently, for example, there is a large outbreak of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, modifying the forest landscape in British Columbia, Canada (Aukema et al. 2006). This outbreak has precipitated concern regarding how major, sudden habitat changes may affect vertebrates such as woodland caribou, *Rangifer tarandus caribou* Gmelin (McNay et al. 2006), but the effects on insect species are less well studied. The present study examines the effects of habitat quality on the spatial distribution and movement of Warren root collar weevil, *Hylobius warreni* Wood (Coleoptera: Curculionidae).

Much of the natural history and ecology of *H. warreni* has been summarized by the pioneering work of G. Warren (1960) and H. Cerezke (1994). In brief, Warren root collar weevils are found throughout the boreal forests of North America, feeding on a variety of conifer tree species. Adults feed on coniferous foliage above-ground. Females lay up to 25

eggs a year in the duff layer around the root collar of trees. Upon eclosion, larvae feed on the phloem tissues of the root collar, protected by a hard casing consisting of a mix of frass and tree resin (Cerezke 1970). After two years of feeding at the root collar, larvae pupate and adults emerge. In the spring months, adults feed nocturnally on young shoots of coniferous trees in preparation for mating and oviposition that occurs throughout the summer and fall (Cerezke 1994). Both male and female Warren root collar weevils are flightless throughout their entire life cycles.

Forest health issues with Warren root collar weevils are predominately related to larval feeding. Adult feeding is not detrimental to the tree host, but larval feeding may inhibit growth, or even result in tree death, by girdling of the stem and disrupting translocation (Cerezke 1974). Although insects do not feed on dead trees, immatures may mature on residual stumps following harvesting, thus supplying weevils to the regenerating forest. Populations are frequently maintained throughout the life of the stand (Cerezke 1973). Mortality to young trees by larval feeding may be exacerbated by root deformation resulting from planting practices (Robert and Lindgren 2006) as well as by root rots introduced at feeding scars (Whitney 1961, 1962).

Hylobius warreni appears to be an emerging concern in forests in western Canada, particularly in areas with extensive ongoing reforestation or regeneration following the current outbreak of mountain pine beetle. While a vast amount of research exists on the ecology and management of related *Hylobius* spp. such as *H. pales* Herbst and *H. radicis* Buchanan (Coleoptera: Curculionidae) in the northeastern United States (Corneil and Wilson 1984, Hunt et al. 1993) and *H. abietis* L. in northern Europe (Nordlander et al. 1997, Leather et al. 1999, Bylund et al. 2004, Nordlander et al. 2005, Wallertz et al. 2006), including

studies on dispersal patterns (Rieske and Raffa 1990, Eidmann 1997), little information exists on the movement or dispersal patterns of *H. warreni* (Schroff et al. 2006).

In this study, we examine the dispersal patterns and movement rates of Warren root collar weevils through different environments containing live and dead trees using a label, release, and recapture experiment. We hypothesize that weevils may exhibit the highest movement rates through habitats with dead trees. Several assumptions underlie the interpretation of dispersal patterns observed. First, we assume that there are no adverse affects of a label used for marking insects (elytral etching, see Methods). Second, we assume that the habitat constructed reflects young stands of lodgepole pine. Third, we assume that the habitat was sufficiently large to allow meaningful observation of dispersal patterns. Fourth, we assume that our sampling method, a newly designed "Björklund funnel trap", was unbiased in various habitat types.

3.3 Materials and Methods

3.3.1 Collection and labelling of insects

Warren root collar weevils were collected from a ca. 15 year old pine forest near Prince George, British Columbia, Canada (53°55'14"N, 122°49'10"W) using a "Björklund funnel trap" attached to the base of each tree (Björklund, in prep). In brief, these traps exploit the insects' nocturnal feeding behaviour and captures them alive, without chemicals, when they descend from the foliage to rest during dawn hours. Three hundred weevils were collected daily from 8 May 2007 to 5 June 2007 and stored in growth chambers at 7°C to reduce the insects metabolism until experiment initiation (Toivonen and Viiri 2006).

Each weevil was labelled in the laboratory. Insects were secured in Petri dishes using plasticine before etching the labels into the elytra with a high speed Dremel® rotary drill (Winder 2004) engraving cutter bit # 106. To accentuate markings, elytral etchings were traced using non-toxic latex-based model paint (Fig. 3.1). Each weevil was labelled with a unique dot-and-number code representing 0-99 in either blue, green, or yellow. To investigate whether labelling affected insect survival, 12 labelled and 12 unlabelled weevils were placed in Petri dishes (10-cm diameter) containing lodgepole pine clippings and moistened filter paper. New lodgepole pine branches were added every week, and filter paper was moistened as necessary. Insect survival in the groups of labelled and unlabelled insects was monitored over a two week period.

The genders of weevils released for the experiment were not identified, since at the time of these experiments a non-invasive technique for sexing had not yet been developed for this species (Cerezke 1994, but see Öhrn et al. 2008). Dissections of 12 randomly selected weevils captured in the same forest used to source weevils for this experiment revealed approximately equal proportions of males and females (7:5), consistent with previous field observations (Warren 1960).

3.3.2 Plot design and insect release

We established 3 experimental plots at the Prince George Tree Improvement Station, British Columbia, Canada (53°46'18"N, 122°43'4"W), to simulate a mix of different habitat types. The plots were established within uniform grassy areas at least 20 m from any trees, to reduce potential migration of unlabeled feral, weevils into the experimental plots. Plots were 22 m in width and 44 m in length. Each plot contained 200 trees (~5 years old) at 2-m spacing (Fig. 3.2).

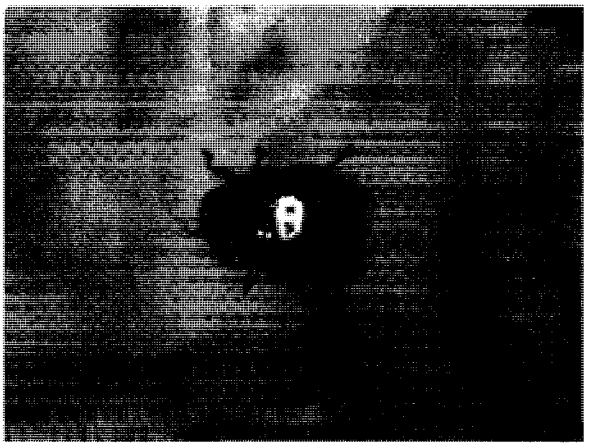


Figure 3.1. Photograph of an adult Warren root collar weevil labelled with a high speed rotory Dremel® drill and latex model paint.

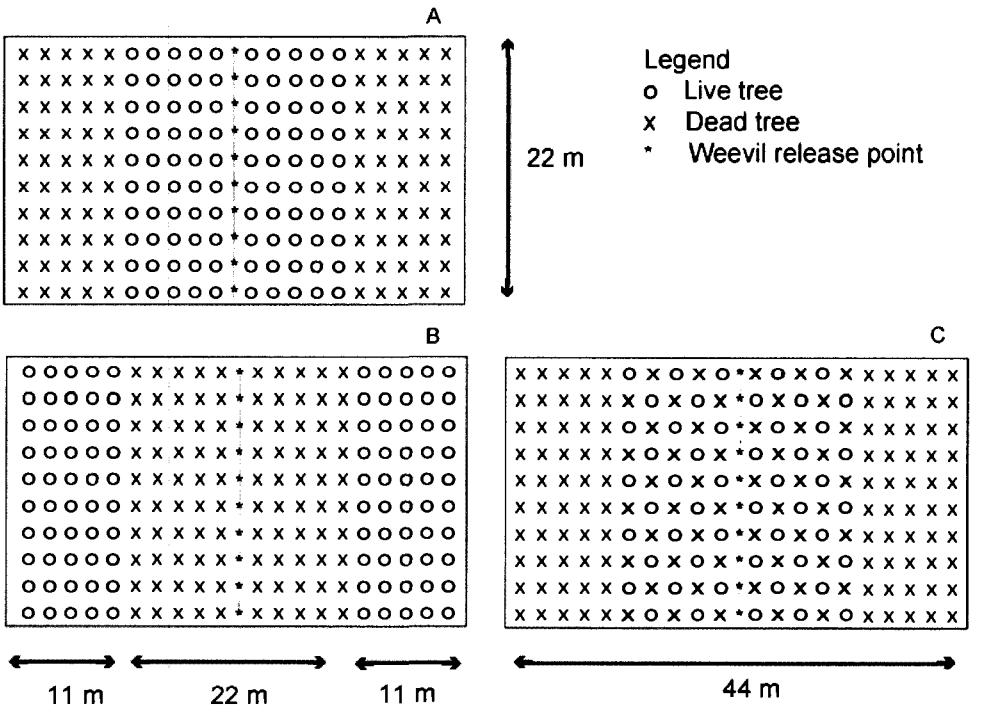


Figure 3.2. Schematic representation of field plots for experiments on habitat discrimination among adult Warren root collar weevil.

The first plot simulated a forest with live trees, adjacent to one with dead trees. The plot was divided into 3 sections with 1 22 x22-m section containing 100 live trees flanked by 2, 11 x22-m sections containing a total of 100 surrogate "dead trees" (Fig. 3.2 A). These dead trees were established by planting dead branches of lodgepole pine of similar size as the live trees, upright into the ground. The second plot simulated a stand of dead trees adjacent to live trees. It was also divided into 3 sections, but was comprised of one 22 x22-m section containing 100 surrogate dead trees and two 11 x22-m sections on either side containing a total of 100 live trees (Fig. 3.2 B). The third plot simulated a stand with a high percentage of dead trees adjacent to a stand with solely dead trees. The plot was divided into 3 sections similar to the first plot (Fig. 3.2 C), but half of the live trees were replaced with surrogate dead trees so that there was a 4-m spacing of live trees.

In each plot, a "Björklund funnel trap" (Björklund, in prep) was installed on each live tree and each dead tree. Traps were placed on dead trees as well as live trees because previous laboratory assays indicated that weevils may be as likely to climb dead vs. live trees (Klingenberg and Aukema, unpublished).

On 14 June 2007 approximately 100 labelled weevils were released along a centre line in each of the plots (95, 92, and 101 insects in each of the plots of Fig 3.2 A, B and C respectively). Plots received unequal numbers due to mislabelling and weevil escapes post-labelling. Approximately 10 weevils were released every 2 -m. Weevil captures were recorded daily on each tree for 8 days and then checked approximately every other day until 13 July for a total of 19 sample collections over 28 days. Following a capture event, the weevil was re-released at the root collar of the tree at which it was trapped. A small number of insects other than weevils (throughout the experiment < 100 in total) were also captured in the traps (results not presented). Following recording, these insects were always released

back into the plot. Some live trees became infested with *Pityogenes* spp. and *Ips* spp. bark beetles (Coleoptera: Curculionidae: Scolytinae) during the course of the experiment. In these cases, the locations were noted to facilitate testing for potential relationships between Warren root collar weevil preference and bark beetles.

3.3.3 Statistical analysis

The likelihood of a tree capturing a weevil was examined using logistic regression, with presence/absence of a weevil in each trap for each day as the binary response variable. Data collected within each of the 3 plots were analysed separately. Each analysis included the explanatory variables of horizontal distance from the release line (1-19 m), vertical distance from the capture to the nearest top/bottom plot margin (0-8 m), number of days since release, habitat type in each section of the experimental plots (live, dead or mixed trees), initial release density to account for small variation in the number of adults released, side of the release line (i.e., left/right, to test for directional dispersal to rising sun, for example), presence/absence of bark beetles, and whether the tree was alive or dead. A backwards elimination procedure was used to remove least-significant variables successively from models. Certain variables tended to be highly collinear (e.g., flanking habitat type in a plot and distance of a tree from the centre insect release line). Hence, even when one of these "masking" variables was removed early in variable selection, we would re-fit similar models *post hoc* substituting the highly correlated variable. Regardless of selection technique, results converged to a single model with lowest AIC value of all models and all remaining variables significant at $\alpha = 0.05$.

The probability of capture is distinct from movement rate. To examine potential differences in movement rates when weevils were released in live, dead, or mixed

habitats, we analysed the horizontal distance travelled vs. number of days following release for all initial captures. This analysis was restricted to capture events recorded within the first 11 days of the experiment, because greater than 80% of the capture events occurred within this time. Moreover, this restriction excluded subsequent captures for any given insect to avoid capture bias (i.e., a few insects were captured more than once, see Results). Data were analysed using analysis of covariance, where horizontal distance from release line was the response variable, number of days post release was the covariate, and habitat type was the factor. In such ANCOVA models, the slope of each line is the movement rate for insects released in a given habitat in meters per day, and the intercept(s) represent *a priori* distance(s) moved by the insect immediately upon release at t=0.

There are different parameterizations of ANCOVA models – each with different ecological meaning – depending on which terms are retained in the model. Models exhibiting uniform or disparate intercepts and slopes can be constructed by including or omitting the covariate (i.e., yielding slope estimates of movement rate(s), the factor (i.e., providing additive *a priori* movement(s) depending on habitat types), and the covariate by factor interaction (i.e., yielding non-parallel lines, or dissimilar movement rates between habitat types). In an ANCOVA model, removing the factor, sometimes called a main effect, is generally not advisable, especially when retaining the interaction term. There are rare instances where this is permissible, however, such as when the factor is not an experimental blocking factor and/or there are valid ecological reasons for a model to have a common intercept but disparate slopes. Here, it seems plausible that all insects move one set distance upon release (such as to an initial tree). Moreover, we were less interested in the effect of habitat type on total movement but rather whether habitat type influenced movement rate. Hence, we fit this model, as well as all other possible ANCOVA parameterizations, including

forcing a common intercept through zero (indicating stationary insects immediately upon release). The model with the highest adjusted R^2 was chosen as the most suitable model (Graham 2003), in conjunction with examinations of residual plots to assess assumptions of normality of errors and homoscedasticity. Where differences among movement rates existed, comparisons were performed using linear contrasts setting α=0.05. All data analysis was conducted in R v.2.6.2 (Ihaka and Gentleman 1996, R Development Core Team 2008).

3.4 Results

The elytral etching and labelling technique did not reduce the survival of weevils. In our preliminary laboratory assay, no mortality was observed in either the labelled or twelve unlabelled groups after a period of 2 weeks (Klingenberg and Aukema, unpublished). We cannot preclude that the labelling technique did not increase visual apparency to predators or decrease insect fitness. We consider these possibilities unlikely, however, as adults insects feed at night and are concealed in the duff during the day, and elytral scratching is unlikely to impact ovariole development. Moreover, this labelling technique has been used successfully with smaller insects such as carabids (Winder 2004).

A total of 101 of the 288 weevils initially released were recaptured over the 28 days, a recovery rate of 35.1 % (Fig. 3.3). Twelve of these weevils were captured more than once. One weevil was captured four times, and one weevil was captured three times in total. The number of weevils captured peaked on the fourth day of the experiment, while the last recorded capture occurred on day 19. Weevils were captured throughout each of the 3 plots. The first place a weevil was captured ranged between 1 and 17 m from the initial release locations (Fig 3.2). On average weevils, released in habitats with live trees (plot A in Fig. 3.2) moved 6.9 m, compared to 9.6 m when released into a habitat of dead trees (plot B in Fig

3.2). Insects released in a habitat of mixed live and dead trees (plot C in Fig 3.2) moved, on average, 5.7 m before their first capture. The furthest that any weevil moved in one day was 15 m.

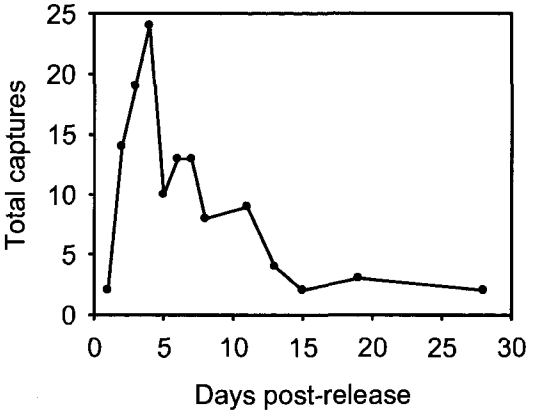


Figure 3.3. Total number of weevil captures following initial release on 14 June 2007. Captures are summed over all plots.

In general, weevil capture was affected by 2 variables: horizontal distance from the release line and time since initial release (Fig. 3.4). The probabilities of capture declined with distance from the release line and days since release when weevils were released in the live and mixed habitats (Fig. 3.4 A, C). In the plot where weevils were released among dead trees, however, only time since release was a significant predictor of likelihood of a tree capturing an insect (Fig. 3.4 B). Variables that were not significant in explaining the likelihood of insect capture included horizontal distance to the nearest margin, initial density of weevils released, side of the release line, presence of bark beetles in the stems of live trees, and the status of individual trees (live/dead).

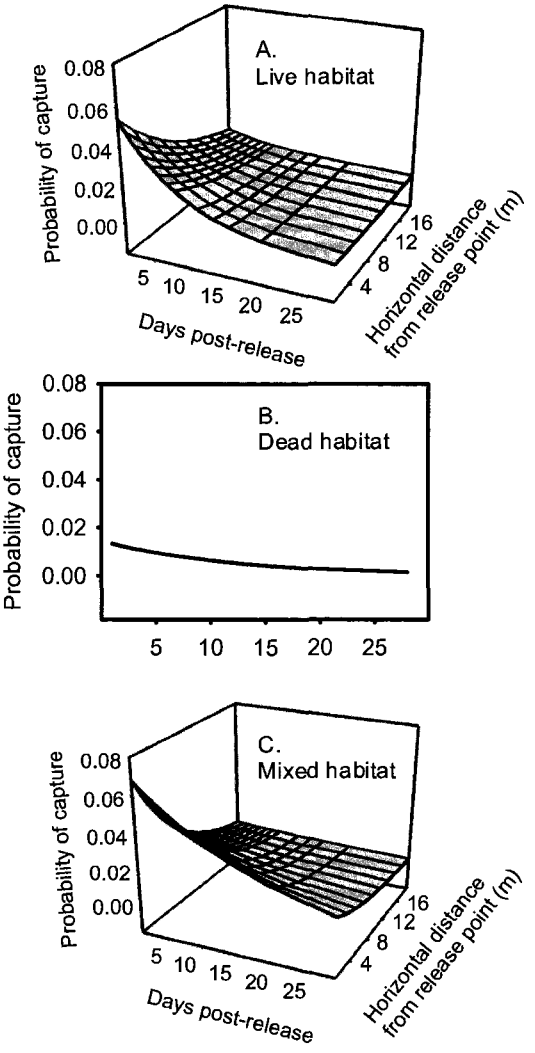


Figure 3.4. Effect of time since initial release (in days) and horizontal distance from release line (in m) on the probability of capturing a weevil on an individual tree in three experimental plots. Each figure label refers to habitat type in centre of plot where the insects were released (see Fig. 3.2). Equations for each plot are A: $y = -2.65 \pm 0.37 - 0.10 \pm 0.034$ (distance) - 0.13 ± 0.040 (time); B: $y = -4.23 \pm 0.34 - 0.081 \pm 0.040$ (time); C: $y = -2.42 \pm 0.30 - 0.15 \pm 0.031$ (distance) - 0.057 ± 0.024 (time), For all equations, probabilities may be obtained by back-transforming values $\exp^y/1 + \exp^y$ (i.e., back-transforming the logit link characteristic of logistic regression).

Movement rate, defined as the relationship between horizontal distance travelled from the release line and time since release to initial capture, varied between the experimental habitat types (Table 3.1). These results are shown graphically in Fig. 3.5.

Table 3.1. ANCOVA table for the movement rate of Warren root collar weevils within different habitat types. Overall model: $F_{3,85}=9.162$, $P<0.0001$, $R^2_{adj}=0.24$.

Term	Df	SS	*F*	*P*
Day	1	340.68	18.97	<0.0001
Day:habitat interaction	2	152.91	4.26	0.0173
Residuals	85	1526.37		

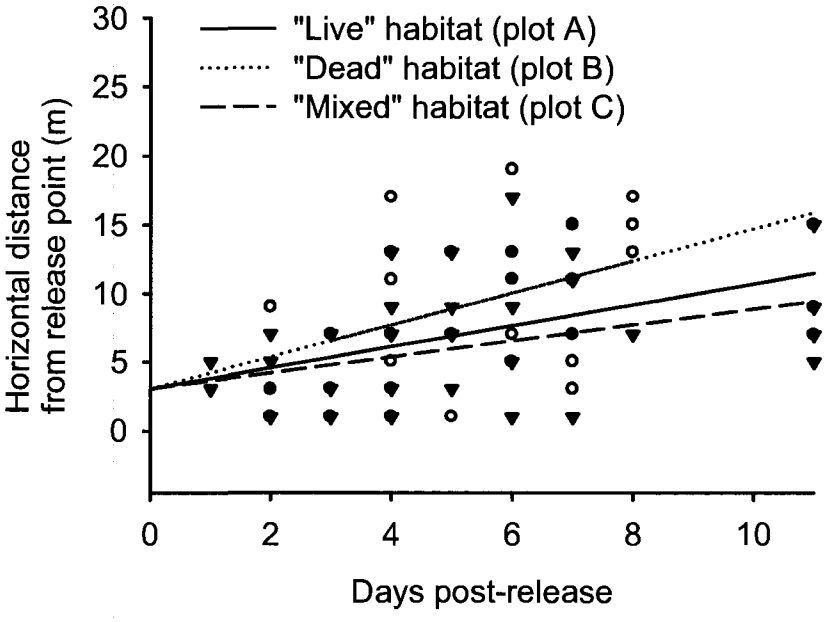


Figure 3.5. Movement rates of Warren root collar weevils released within three experimental plots. The filled in circles and solid regression line represent weevil captures within plot A (insects released in "live" habitat), the open circles and dotted regression line represent captures within plot B (insects released in "dead" habitat), and the triangles and dashed regression line represent captures within plot C (insects released in "mixed" habitat). See text for the equations of lines.

The most suitable model exhibits a common intercept among the three central habitat types in each plot of 3.02 ± 0.99 m. That is, when the insects were released, they appeared to travel 3 m *a priori*. Movement rates varied among habitat types ($F_{2,86}=3.98$; $P < 0.05$). Weevils exhibited the highest movement rates when released into dead habitats (plot B in

Fig. 3.2), moving at 1.17 ± 0.23 m/day. This was significantly higher than movement rates through live (0.77 ± 0.21 m/day) and mixed habitats (0.58 ± 0.18 m/day) (plots A and C, respectively, in Fig. 3.2.) (t_{86}=2.73; P=0.0077).

3.5 Discussion

Our results demonstrate that habitat quality, defined as varying composition of live vs. dead trees, affects the movement and distribution of Warren root collar weevils. Movement rates are elevated in habitats with dead trees and lower in habitats with live trees, providing evidence that Warren root collar weevils may migrate away from areas with high proportions of dead trees and concentrate in areas with live trees. These findings are important within the context of the recent outbreak of mountain pine beetle in British Columbia, which now encompasses more than 13 million ha of mature lodgepole pine forests (Westfall and Ebata 2008). In many areas, extensive salvage harvesting and reforestation efforts give rise to situations where young lodgepole pine forests are planted directly adjacent to unharvested, mature stands with a high percentage of trees killed by mountain pine beetle. A recent study has shown that the proximity and condition of nearby mature stands affected by outbreaking populations of mountain pine beetle is directly proportionate to Warren root collar weevil pressure within young stands (Chapter 2). The current study lends support to a proposed mechanism, i.e., that Warren root collar weevils are migrating out of mature stands heavily affected by mountain pine beetle (i.e., those with few live hosts), and concentrating in these young regenerating stands.

The concentration of Warren root collar weevils within young stands is a substantial concern for regeneration. Almost all coniferous forests contain endemic populations of

Warren root collar weevil (Cerezke 1967). For example, observations of young lodgepole pine forests in the central interior of British Columbia have found levels of mortality due to Warren root collar weevil as high as 16% (Schroff et al. 2006). Migration of Warren root collar weevils from surrounding mature stands into a reforested area stocked with young trees may add to pressure from populations that have developed from immatures left on stumps following harvesting operations (Cerezke 1973). Such increases in tree mortality may limit the ability of forest managers to obtain a "free to grow" status, whereby they can return responsibility of the forests to government organizations.

Previous studies have indicated that Warren root collar weevil may disperse 2.3 m, on average, during one night (Cerezke 1994). This is twice the average movement rates we observed, i.e., 1.17 m/day, when insects were released into the plots with dead trees in the centre. The previous findings, however, were collected in juvenile forests with trees that were significantly larger than those used in our field experiments. It is possible that weevils exhibit higher movement rates between larger trees, perhaps due to increased tree spacing as the stand thins with age (naturally or anthropogenically). Insects may exhibit higher movement rates in open spaces to escape predation, for example (Denno et al. 1990). If weevils exhibit higher movement rates between larger trees, then migration out of forests with high proportions of trees killed by mountain pine beetle would be enhanced not only by dead trees, but also those with larger diameters and spacings. Mountain pine beetle typically kills the largest trees in the course of an outbreak (Amman 1972, Safranyik et al. 1974, Cole et al. 1976, Amman 1984), potentially exacerbating this migration event.

Temporally, the probability of a tree capturing a weevil declined during the course of the experiment in all three plots as the insects dispersed, and weevils were progressively less likely to be captured within a habitat patch. Previously, it was thought that adult Warren root

collar weevils may move up to 13 m during one season (Henigman et al. 2001). Given that females are engaged in host-seeking and ovipositional behaviour for approximately 100 days in the summer months (Cerezke 1994), and our findings that insects may move 10-15 m in one night, it is not improbable that these insects move 50-100 m a year or more, depending on habitat conditions.

Spatially, not surprisingly, the probability of individual trees capturing weevils was highest in plots with live trees close to the release location (i.e. plots A and C with live and mixed habitats into the centre (Fig. 3.4 A, C)). There was no effect of distance on capture probability when insects were released into the habitat with dead trees in the centre (Fig. 3.4 B). This is likely because the insects dispersed so rapidly through this habitat with dead trees, exhibiting the highest movement rates of 1.17 m/day in this plot (Fig. 3.5). An alternative, but not mutually exclusive, explanation is that the lack of distance effect is an artefact of capture bias on live vs. dead trees, as both plots where distance effects were exhibited (live and mixed habitats in centre) contained live trees proximate to the release lines. Since Warren root collar weevil do not feed on dead trees, insects would likely arrest more frequently on live trees, thus decreasing apparent movement rates. We note, however, that insects were occasionally trapped on dead trees in the mixed habitat, such that there was no statistical difference between live and dead trees for the probability of capture in that plot ($P > 0.05$). Presumably, then, dispersal rate is elevated in dead habitats vs. live habitats.

The initial lateral distance travelled by an insect prior to capture, regardless of habitat type, was 3 m (i.e., intercept in Fig. 3.5). Because the first 2 rows of trees are located at 1 and 3 m from the release location, this finding is in accordance with the plot design. *A priori* movement of 3 m suggests that when a group of weevils are released, they move this set distance to a tree to reduce crowding. We lack data, however, on how fluctuating population

densities at a larger scale (e.g., cutblock level) may affect movement rates via crowding or competition for resources (either feeding or ovipositional). Moreover, our experiment was not designed to test potential saturation levels that may inhibit movement in natural, field settings.

This study represents the first deployment of the novel "Björklund funnel trap" for large-scale trapping of a walking weevil. Previous research on this insect has been hampered by the lack of a simple, cost-effective, easy-to-deploy trapping or sampling method (Cerezke 1994). Currently, there are no known chemical attractants for Warren root collar weevils. In contrast, studies with *H. radicis* in the eastern United States and *H. abietis* in Northern Europe using established trapping methodologies have facilitated discovery of chemical attractants such as ethanol and terpenes (Hunt and Raffa 1989, Nordlander 1990, Hoffman et al. 1997, Björklund et al. 2005). Future capture and release studies using the "Björklund" funnel trap may identify possible chemical attractants or anti-feedants (Månsson et al. 2005), refine trap efficacy (Rieske and Raffa 1999), and provide population estimates within forest habitats (Rieske and Raffa 1993). Such research could facilitate a better understanding of the biological mechanisms controlling Warren root collar weevil dispersal and host selection.

3.6 Acknowledgements

We would like to thank the "LAPH" forest entomology research cluster (laboratories of B.S. Lindgren, B.H. Aukema, L. Poirier and D. Huber) at the University of Northern British Columbia for fruitful discussions and ideas. We thank R. Wagner and staff at the Prince George Tree Improvement Station for logistical and field support. We also thank Sandy Allen, Hollie Moore, Gareth Hopkins, Fraser McKee, Honey Giroday, Sean Henderson and Jeff Selesnic for help with field operations. This research was supported by a

British Columbia Forest Science Program grant M086046, the Canadian Forest Service, and Pacific Forestry Centre Graduate, Canfor Industries Graduate and UNBC Graduate awards to MDK.

3.7 Literature Cited

Amman, G. D. 1972. Mountain pine beetle (Coleoptera-Scolytidae) brood production in relation to thickness of lodgepole pine phloem. Journal of Economic Entomology **65**:138-&.

Amman, G. D. 1984. Mountain pine-beetle (Coleoptera: Scolytidae) mortality in 3 types of infestations. Environmental Entomology **13**:184-191.

Aukema, B. H., A. L. Carroll, J. Zhu, K. F. Raffa, T. A. Sickley, and S. W. Taylor. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. Ecography **29**:427-441.

Bengtsson, J., T. Persson, and H. Lundkvist. 1997. Long-term effects of logging residue addition and removal on macroarthropods and enchytraeids. Journal of Applied Ecology **34**:1014-1022.

Bergeron, Y., A. Leduc, B. D. Harvey, and S. Gauthier. 2002. Natural fire regime: A guide for sustainable management of the Canadian boreal forest. Silva Fennica **36**:81-95.

Björklund, N., G. Nordlander, and H. Bylund. 2005. Olfactory and visual stimuli used in orientation to conifer seedlings by the pine weevil, *Hylobius abietis*. Physiological Entomology **30**:225-231.

Blossey, B. and T. R. Hunt-Joshi. 2003. Belowground herbivory by insects: Influence on plants and aboveground herbivores. Annual Review of Entomology **48**:521-547.

Burton, P. J. 2002. Effects of clearcut edges on trees in the sub-boreal spruce zone of Northwest-Central British Columbia. Silva Fennica **36**:329-352.

Bylund, H., G. Nordlander, and H. Nordenhem. 2004. Feeding and oviposition rates in the pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). Bulletin of Entomological Research **94**:307-317.

Cerezke, H. F. 1967. A method for rearing root weevil, *Hylobius warreni* (Coleoptera: Curculionidae). Canadian Entomologist **99**:1087-1090.

Cerezke, H. F. 1970. Method for estimating abundance of weevil, *Hylobius warreni* Wood, and its damage in lodgepole pine stands. Forestry Chronicle **46**:392-396.

Cerezke, H. F. 1973. Survival of the weevil, *Hylobius warreni* Wood, in lodgepole pine stumps. Canadian Journal of Forest Research **3**:367-372.

Cerezke, H. F. 1974. Effects of partial girdling on growth in lodgepole pine with application to damage by the weevil *Hylobius warreni* Wood. Canadian Journal of Forest Research **4**:312-320.

Cerezke, H. F. 1994. Warren rootcollar weevil, *Hylobius warreni* Wood (Coleoptera: Cuculionidae), in Canada: ecology, behaviour, damage relationships, and management. Canadian Entomologist **126**:1383-1442.

Cole, W. E., G. D. Amman, and C. E. Jensen. 1976. Mathematical-models for mountain pine beetle lodgepole pine interaction. Environmental Entomology **5**:11-19.

Corneil, J. A. and L. F. Wilson. 1984. Dispersion and seasonal activity of the pales weevil, *Hylobius-pales* (Coleoptera: Curculionidae), in Michigan christmas tree plantations. Canadian Entomologist **116**:711-717.

DeLong, S. C. 2002. Using nature's template to best advantage in the Canadian boreal forest. Silva Fennica **36**:401-408.

Denno, R. F., S. Larsson, and K. L. Olmstead. 1990. Role of enemy-free space and plant-quality in host-plant selection by willow beetles. Ecology **71**:124-137.

Denno, R. F., M. S. McClure, and J. R. Ott. 1995. Interspecific interactions in phytophagous insects - competition reexamined and resurrected. Annual Review of Entomology **40**:297-331.

Diggle, P. 1985. A kernel-method for smoothing point process data. Applied Statistics-Journal of the Royal Statistical Society Series C **34**:138-147.

Duke, L. and B. S. Lindgren. 2006. Attack by *Hylobius warreni* on grafted lodgepole pine and its relationship with monoterpene composition and scion: rootstock diameter ratio. Agricultural and Forest Entomology **8**:305-311.

Eidmann, H. H. 1997. Assessment of pine weevil numbers on clear-cut and forest sites with shelter boards and pitfall traps. Anzeiger Fur Schadlingskunde Pflanzenschutz Umweltschutz **70**:68-72.

Haynes, K. J. and J. T. Cronin. 2003. Matrix composition affects the spatial ecology of a prairie planthopper. Ecology **84**:2856-2866.

Haynes, K. J. and J. T. Cronin. 2006. Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. Oikos **113**:43-54.

Heliölä, J., M. Koivula, and J. Niemelä. 2001. Distribution of Carabid beetles (Coleoptera: Carabidae) across a boreal forest-clearcut ecotone. Conservation Biology **15**:370-377.

Henigman, J., T. Ebata, E. Allen, J. Westfall, and A. Pollard. 2001. Field guide to forest damage in British Columbia. British Columbia Ministry of Forests and the Canadian Forest Service, Victoria, BC.

Hicke, J. A., J. A. Logan, J. Powell, and D. S. Ojima. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. Journal of Geophysical Research-Biogeosciences **111**.

Hoffman, G. D., D. W. A. Hunt, S. M. Salom, and K. F. Raffa. 1997. Reproductive readiness and niche differences affect responses of conifer root weevils (Coleoptera: Curculionidae) to simulated host odors. Environmental Entomology **26**:91-100.

Hopkins, G. R., M. D. Klingenberg, and B. H. Aukema. 2008. Feeding and ovipositional behaviour of *Hylobius warreni* Wood (Coleoptera: Curculionidae) on host and non-host bark in laboratory bioassays. Agricultural and Forest Entomology:Accepted pending revisions.

Hunt, D. W. A., G. Lintereur, S. M. Salom, and K. F. Raffa. 1993. Performance and preference of *Hylobius radicis* Buchanan, and *H pales* (Herbst) (Coleoptera: Curculionidae) on various pinus species. Canadian Entomologist **125**:1003-1010.

Hunt, D. W. A. and K. F. Raffa. 1989. Attraction of *Hylobius radicis* and *Pachylobius picivorus* (Coleoptera: Curculionidae) to ethanol and turpentine in pitfall traps. Environmental Entomology **81**:351-355.

Ihaka, I. and R. Gentleman. 1996. R: a language for data analysis and graphics. Journal of Computational Graphical Statistics **5**:299-314.

Latty, E. F., S. M. Werner, D. J. Mladenoff, K. F. Raffa, and T. A. Sickley. 2006. Response of ground beetle (Carabidae) assemblages to logging history in northern hardwood-hemlock forests. Forest Ecology and Management **222**:335-347.

Leather, S. R., S. I. Ahmed, and L. Hogan. 1994. Adult feeding preferences of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae). European Journal of Entomology **91**:385-389.

Leather, S. R., K. R. Day, and A. N. Salisbury. 1999. The biology and ecology of the large pine weevil, *Hylobius abietis* (Coleoptera : Curculionidae): a problem of dispersal? Bulletin of Entomological Research **89**:3-16.

Lemieux, J. P. and B. S. Lindgren. 2004. Ground beetle responses to patch retention harvesting in high elevation forests of British Columbia. Ecography **27**:557-566.

Månsson, P. E., C. Eriksson, and K. Sjödin. 2005. Antifeedants against *Hylobius abietis* pine weevils: An active compound in extract of bark of *Tilia cordata* linden. Journal of Chemical Ecology **31**:989-1001.

Månsson, P. E. and F. Schlyter. 2004. *Hylobius* pine weevils adult host selection and antifeedants: feeding behaviour on host and non-host woody scandinavian plants. Agricultural and Forest Entomology **6**:165-171.

Matsuoka, S. M., C. M. Handel, and D. R. Ruthrauff. 2001. Densities of breeding birds and changes in vegetation in an Alaskan boreal forest following a massive disturbance by spruce beetles. Canadian Journal of Zoology **79**:1678-1690.

McNay, R. S., B. G. Marcot, V. Brumovsky, and R. Ellis. 2006. A Bayesian approach to evaluating habitat for woodland caribou in north-central British Columbia. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **36**:3117-3133.

Meidinger, D. and J. Pojar. 1991. Ecosystems of British Columbia, Special Report Series 6. BC Ministry of Forests **Victoria, BC.**

Nathan, R., G. Perry, J. T. Cronin, A. E. Strand, and M. L. Cain. 2003. Methods for estimating long-distance dispersal. Oikos **103**:261-273.

Negron, J. F. 1998. Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. Forest Ecology and Management **107**:71-85.

Niemelä, J., D. Langor, and J. R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conservation Biology **7**:551-561.

Nordlander, G. 1990. Limonene inhibits attraction to alpha-pinene in the pine weevils *Hylobius-abietis* and *H-pinastri*. Journal of Chemical Ecology **16**:1307-1320.

Nordlander, G., H. Bylund, and N. Björklund. 2005. Soil type and microtopography influencing feeding above and below ground by the pine weevil *Hylobius abietis*. Agricultural and Forest Entomology **7**:107-113.

Nordlander, G., H. Bylund, G. Örlander, and K. Wallertz. 2003. Pine weevil population density and damage to coniferous seedlings in a regeneration area with and without shelterwood. Scandinavian Journal of Forest Research **18**:438-448.

Nordlander, G., H. Nordenhem, and H. Bylund. 1997. Oviposition patterns of the pine weevil *Hylobius abietis*. Entomologia Experimentalis Et Applicata **85**:1-9.

Phillips, I. D., T. P. Cobb, J. R. Spence, and R. M. Brigham. 2006. Salvage logging, edge effects, and carabid beetles: Connections to conservation and sustainable forest management. Environmental Entomology **35**:950-957.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org.

Raffa, K. F., S. C. Krause, and P. B. Reich. 1998. Long-term effects of defoliation on red pine suitability to insects feeding on diverse plant tissues. Ecology **79**:2352-2364.

Rieske, L. K. and K. F. Raffa. 1990. Dispersal patterns and mark-and-recapture estimates of 2 pine root weevil species, *Hylobius pales* and *Pachylobius picivorus* (Coleoptera: Curculionidae), in christmas tree plantations. Environmental Entomology **19**:1829-1836.

Rieske, L. K. and K. F. Raffa. 1993. Potential use of baited pitfall traps in monitoring pine root weevil, *Hylobius pales*, *Pachylobius picivorus*, and *Hylobius radicis* (Coleoptera: Curculionidae) populations and infestation levels. Journal of Economic Entomology **86**:475-485.

Rieske, L. K. and K. F. Raffa. 1999. Baited pitfall traps and evaluation of dispensing methods for root weevils (Coleoptera: Curculionidae) in newly established pine plantations in Wisconsin. Journal of Economic Entomology **92**:439-444.

Robert, J. A. and B. S. Lindgren. 2006. Relationships between root form and growth, stability, and mortality in planted versus naturally regenerated lodgepole pine in north-central British Columbia. Canadian Journal of Forest Research **36**:2642-2653.

Safranyik, L., D. M. Shrimpton, and H. S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Forestry Technical Report 1, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia **1**:1-23.

Schroff, A. Z., B. S. Lindgren, and M. P. Gillingham. 2006. Random acts of weevil: A spatial analysis of *Hylobius warreni* attack on *Pinus contorta* var. *latifolia* in the sub-boreal spruce zone of Northern British Columbia. Forest Ecology and Management **227**:42-49.

Shore, T. L. and L. Safranyik. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Forestry Canada, Pacific and Yukon Region, Pacific Forestry Centre, Victoria British Columbia:1-12.

Sullivan, T. P. and D. S. Sullivan. 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. Journal of Applied Ecology **38**:1234-1252.

Sullivan, T. P., D. S. Sullivan, and P. M. F. Lindgren. 2001. Influence of variable retention harvests on forest ecosystems. I. Diversity of stand structure. Journal of Applied Ecology **38**:1221-1233.

Taylor, S. W., A. L. Carroll, R. I. Alfaro, and L. Safranyik. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre:Victoria, British Columbia.

Toivonen, R. and H. Viiri. 2006. Adult large pine weevils *Hylobius abietis* feed on silver birch *Betula pendula* even in the presence of conifer seedlings. Agricultural and Forest Entomology **8**:121-128.

Wallertz, K., G. Nordlander, and G. Örlander. 2006. Feeding on roots in the humas layer by adult pine weevil, *Hylobius abietis*. Agricultural and Forest Entomology **8**:1-7.

Wallin, K. F. and K. F. Raffa. 2001. Effects of folivory on subcortical plant defenses: Can defense theories predict interguild processes? Ecology **82**:1387-1400.

Warren, G. L. 1956. Root Injury to conifers in Canada by species of *Hylobius* and *Hypomolyx* (Coleoptera: Curculionidae). Forestry Chronicle **March**.

Warren, G. L. 1960. External anatomy of the adult of *Hylobius warreni* Wood (Coleoptera: Curculionidae) and comparison with *H. pinicola* (Couper). The Canadian Entomologist **92**:321-341.

Westfall, J. and T. Ebata. 2008. 2007 Summary of forest health conditions in British Columbia. Library and Archives Canada Cataloguing in Publication Data: Pest Management Report Number 15. BC Ministry of Forests and Range, Victoria, BC.

Whitney, R. D. 1961. Root wounds and associated root rots of white spruce. Forestry Chronicle **37**:401-411.

Whitney, R. D. 1962. Studies in forest pathology. Canadian Journal of Botany **40**:1631-1657.

Winder, L. 2004. Marking by abrasion or branding and recapturing carabid beetles in studies of their movement. International Journal of Pest Management **50**:161-164.

4: CONCLUSIONS AND MANAGEMENT IMPLICATIONS

4.1 Conclusions

Warren root collar weevil is an emerging forest-management concern for young lodgepole pine plantations. Although tree mortality levels have historically remained low (<5 %), with localized exceptions (Byford 1994; Herring and Coates 1981; Schroff *et al.* 2006), recent forest conditions on the landscape of British Columbia have predisposed young stands to elevated levels of mortality resulting from larval feeding of this insect. Following the recent province-wide epidemic of mountain pine beetle, large expanses of mature dead lodgepole pine cover the landscapes of British Columbia (Aukema et al. 2006, Westfall and Ebata 2008). Recently, forestry professionals working with the Ministry of Forests and Range (Ken White and Carolyn Stevens) have noted elevated levels of tree mortality (~40%) around the margins of young lodgepole pine stands (7-15 years of age) adjacent to unsalvaged, mature stands with high levels of mountain pine beetle-induced mortality (>80%). One hypothesis is that populations of Warren root collar weevil are moving from unsalvaged stands with reduced host availability into adjacent replantings. The research presented within this thesis investigates levels of tree mortality resulting from populations of Warren root collar weevil. Moreover, it seeks to elucidate the mechanisms that produce the spatial and temporal patterns of young tree mortality observed.

Chapter 1 introduced previous research done with Warren root collar weevil and briefly outlines similar research done with other *Hylobius* spp of weevil in northern Europe and the eastern United States. Chapter 2 presented data collected within young lodgepole pine stands (9-11 years of age) that quantify tree mortality and draws inference between spatial patterns of young tree mortality and characteristics of adjacent, mature, unsalvaged

stands heavily impacted by outbreaks of mountain pine beetle (>80% mortality). Chapter 3 presented data from a label, release, and recapture experiment to quantify Warren root collar weevil movement in habitats with varying levels of live and dead trees in an attempt to study mechanisms responsible for the patterns of mortality observed.

The ground surveys that I conducted within 9 separate cutblocks revealed that Warren root collar weevil is the primary, causative agent of mortality to young lodgepole pine trees in these replanted cutblocks adjacent to unsalvaged, mature stands that have been killed by mountain pine beetle. The results collected and presented within this thesis show that almost 90% of young lodgepole pine trees (8-11 years of age) that had died had experienced partial to complete girdling by larvae of Warren root collar weevil. The ground surveys demonstrated a gradient of tree mortality from edges of mature, unsalvaged stands into regenerating cutblocks, caused by larval feeding of the Warren root collar weevil, at 100 meter scales. Moreover, within these gradients, Warren root collar weevils were found to prefer the most dominant regenerating trees.

The gradients of young tree mortality were found to be exacerbated by the condition of the adjacent, mature, unsalvaged stands. That is, mortality of young pine, due to Warren root collar weevil larvae feeding, within the cutblocks increases with increasing percentages of pine (80-90%) and dead pine (80-90%) in adjacent unsalvaged mature stands. Moreover, this gradient was found to get progressively worse with increasing time since mountain pine beetle had attacked the adjacent mature stand. These findings indicate that young lodgepole pine mortality due to Warren root collar weevil will be elevated in areas with mature trees attacked and killed by mountain pine beetle, and that the young tree mortality will be higher close to the margins of young replantings.

Similar gradients of young lodgepole pine mortality were found to exist at the scale of the entire cutblock. Analysis of aerial survey data indicated that levels of mortality were elevated around the entire perimeter in 6 of the 9 cutblocks. In two other cutblocks, gradients of mortality existed from at least half of the cutblock edges. Because Warren root collar weevil is the primary cause of mortality in each of these cutblocks, it appears that mortality due to Warren root collar weevils is a widespread problem where unsalavaged stands exist adjacent to replanted cutblocks at the landscape level. In the few instances where consistent gradients of mortality from stand edges were absent, site-specific factors such as retention of residual patches – possibly obscuring weevil movement patterns – or variances in moisture regimes may be altering weevil activity. For example, higher moisture levels favour Warren root collar weevil development (Cerezke 1994).

To determine specific mechanisms of Warren root collar weevil dispersal from habitats with high percentages of dead lodgepole pine into habitats with live trees, I conducted a movement study in young lodgepole pine stands (~5 years old). The movement study was conducted with 300 adult Warren root collar weevils, each labelled with a unique marker. Their location of release and location of each recapture was recorded to monitor movement during the 28 day experiment. Three research plots were established, each with 200 trees planted at 2-m spacing. Three habitat types were tested, with each of the 3 plots containing 2 separate habitat types each. The 3 habitats types included live habitats containing only live trees, dead habitats containing only dead trees, and a mixed habitat containing dead and live trees. Each plot had a different habitat proximal to the release location to monitor differences in dispersal in each habitat type. The results from this study show that Warren root collar weevils exhibit higher rates of movement in habitats of dead trees vs. live trees. Based on these findings, I conclude that the patterns of young tree

mortality observed from the ground surveys conducted within cutblocks (Chapter 2) are influenced by the movement of Warren root collar weevils from mature stands killed by mountain pine beetle into adjacent, young replantings of lodgepole pine.

I conclude that Warren root collar weevils are moving from unsalvaged, mature stands of lodgepole pine with reduced host pools into adjacent, regenerating cutblocks. The ground and aerial surveys (Chapter 2) conducted have shown significant gradients of mortality within cutblocks as well as correlated levels of mortality of young trees with the levels of mortality within adjacent mature lodgepole pine stands. The movement studies have shown that Warren root collar weevils will disperse from areas with dead trees into areas with live trees (Chapter 3) suggesting that patterns of tree mortality observed from ground and aerial surveys are caused by the mass movement of Warren root collar weevils from unsalvaged mature stands recently killed by mountain pine beetle to adjacent, young replantings. This phenomenon may pose serious challenges to forest management in the wake of the current mountain pine beetle epidemic.

4.2 Management Implications and Silvicultural Recommendations

The following suggestions to mitigate impacts by Warren root collar weevil are compiled from previous work done by H. Cerezke (1994), G. T. Byford (1994) and Herring and Coates (1981) and are modified by the findings presented within this thesis. These recommendations may be useful for mitigating future mortality induced by Warren root collar weevils following the recent outbreak of mountain pine beetle.

The first recommendation is to conduct assessments to quantify the potential for reforestation challenges as a result of Warren root collar weevil populations prior to replanting. These assessments should first quantify population levels of Warren root collar

weevil and then quantify the condition of the residual mature stands. Insect abundance may be estimated using destructive sampling of lodgepole pine trees (Byford 1994), as well as non-destructive sampling using the "Björklund funnel trap" presented in this thesis (Appendix B). Quantifying the condition of mature stands may indicate relative risk of weevil populations migrating from the mature stands into the young replantings. If the residual mature stand contains a high percentage of lodgepole pine (>80%), of which a large component is dead (>80%), populations of Warren root collar weevil may migrate from these stands into the nearby young regenerating stands (Chapter 2 and Chapter 3). These pre-planting assessments will identify the potential for populations of Warren root collar weevil migrating from residual mature stands into young replantings and help determine if further silvicultural treatments are needed to mitigate young tree mortality due to Warren root collar weevil larvae feeding. Developing robust population estimates from new sampling methodologies such as the "Björklund funnel trap" is a critical area of future research, however.

The second recommendation is to employ post-harvest management strategies to limit the development of residual eggs and larvae from Warren root collar weevils. Removal of these populations is important because it takes up to two years for the development of eggs and larvae left within cutblocks to develop into adults. Adults may live up to 5 years, resulting in populations that may be maintained for 7 years following the harvesting of mature stands. For example, one strategy would include the burning of slash following harvest to reduce the duff layer, amenable to weevil populations, and kill residual egg and larval weevils developing on stumps (Cerezke 1994). Moreover, if replanting is delayed 2 to 3 years, fecundity and oviposition by the long-lived females may be reduced or adults may vacate the cutblocks in search of food. These techniques will reduce the development of

populations within cutblocks although admittedly may not affect the migration of weevils from adjacent stands.

The third recommendation is to modify planting standards to reduce future mortality due to Warren root collar weevil. Although these insects may feed on a variety of coniferous hosts (Cerezke 1994), planting a mix of preferred (lodgepole pine) and non-preferred hosts (hybrid spruce, Douglas-fir, etc.) may reduce the development of Warren root collar weevil within young stands. Adult weevils prefer feeding on pine vs. spruce and trembling aspen in laboratory assays using cut branches (Hopkins et al., 2008). These preferences may persist in field settings and reflect ovipositional preference as well. Maintenance of high stocking standards (>1600 stems/ha) may also reduce levels of young tree mortality due to feeding by Warren root collar weevil larvae (Cerezke 1994). Higher density of trees has been shown to create micro-site conditions that hinder the development of this weevil.

Following the recent province wide outbreak of mountain pine beetle, regeneration of merchantable forests for tomorrow will depend upon limiting insect challenges such as Warren root collar weevil. The results presented within this thesis have shown that Warren root collar weevil is a concern to regenerating pine stands across the central interior of British Columbia (i.e., Quesnel, Vanderhoof, Nadina and Prince George forest districts) (Chapter 2). Warren root collar weevil- induced young tree mortality was also found to be correlated with the percent mortality of adjacent mature lodgepole pine stands as shown by the concentration of mortality towards the margins of cutblocks (Chapter 2). The results presented indicate that the patterns of mortality observed are connected to the migration of Warren root collar weevils from adjacent mature lodgepole pine stands recently killed by mountain pine beetle (Chapter 3). The recommendations of post-harvest assessment, scarification treatments and modifying stocking standards will be useful tools for the management of future forests.

4.3 Literature Cited

Byford, G. T., editor. 1994. Warren's Collar Weevil in lodgepole pine stands in the Kispiox forest district. The University of Northern British Columbia, Prince George, British Columbia.

Cerezke, H. F. 1994. Warren rootcollar weevil, *Hylobius warreni* Wood (Coleoptera: Cuculionidae), in Canada: ecology, behaviour, damage relationships, and management. Canadian Entomologist **126**:1383-1442.

Herring, L. J. and H. G. Coates, editors. 1981. Warren's Collar Weevil: The underground plantation menace. Province of British Columbia, Ministry of Forests, Prince George, BC.

Hopkins, G. R., M. D. Klingenberg, and B. H. Aukema. 2008. Feeding and ovipositional behaviour of *Hylobius warreni* Wood (Coleoptera: Curculionidae) on host and non-host bark in laboratory bioassays. Agricultural and Forest Entomology: Accepted pending revisions.

Schroff, A. Z., B. S. Lindgren, and M. P. Gillingham. 2006. Random acts of weevil: A spatial analysis of *Hylobius warreni* attack on *Pinus contorta* var. *latifolia* in the sub-boreal spruce zone of Northern British Columbia. Forest Ecology and Management **227**:42-49.

Westfall, J. and T. Ebata. 2008. 2007 Summary of forest health conditions in British Columbia. Library and Archives Canada Cataloguing in Publication Data: Pest Management Report Number 15. BC Ministry of Forests and Range, Victoria, BC.

APPENDIX A

The following code is included as a resource for future students and professionals. The code (A.1 and A.2) outlined and the graphical representations of cutblocks (Table A.1) provide methodological detail to supplement the analyses outlined in Chapters 2 and 3.

A.1 R code and abbreviated programming notes for Chapter 2: Links between above- and below-ground herbivory and challenges to forest management: Landscape-level impacts of Warren root collar weevil following mountain pine beetle

1. Load packages

```
library(spatstat)
```
(Diggle 1985)

```
# load the Spatial Statistics Package.

library(maptools)
# load the Map Tools Package.

# each cutblock was analyzed separately using spatial data for each dead tree that I
imported from Arcview v. 9.2. The outline for each cutblock was loaded into R using
a shapefile of the boundary. Residual stands within each cutblock (i.e. holes) were
imported separately.
```

2. Read in data

```
data <-read.table("points.txt", header=T, sep="\t", na.strings="NA")
# load the spatial data (with x and y coordinates) for each cutblock.
```

3. Convert the data points to meters

```
data$X <- data$x/conversion factor
```
(number depends on the dimensions and GSD (ground sampling distance) of the cutblock)

```
data$Y <- data$y/conversion factor
```
(number depends on the dimensions and GSD (ground sampling distance) of the cutblock)

4. Load the shapefile outline

```
cutblock <- read.shape("cutblock.shp")
```

5. Load the shapefile outline of each residual patch to be cut from the original outline (if applicable, i.e., if the cutblock has residual patches)

```
cutblockholesmap <- read.shape("cutblockwithholes.shp")
```

6. Plot the shapefile outline (for visual inspection)

```
plot(cutblock)
```

7. Plot the shapefile outline of the residual patche(s)

```
plot(cutblockholesmap)
```

8. Create vertices from shapefile outline of residual plots

```
hole1x <- cutblockholesmap$Shapes[[2]]$verts[-1,1];
hole1y <- cutblockholesmap$Shapes[[2]]$verts[-1,2]
```

9. Convert dimensions of shapefile for each residual (each hole in the cutblock)

```
hole1x <- hole1x/conversion factor (number depends on the dimensions and
GSD (ground sampling distance) of the cutblock)
hole1y <- hole1y/conversion factor (number depends on the dimensions and
GSD (ground sampling distance of the cutblock)
```

10. Create vertices from the shapefile outline and convert the shapefile dimensions to the same units as the point coordinates for dead trees

```
vertices <- map$Shapes[[1]]$verts
vertices <- vertices[-1,]
boundary.x <- (vertices[,1])
boundary.y <- (vertices[,2])
boundary.x <- boundary.x/conversion factor(number depends on the dimensions
and GSD (ground sampling distance) of the cutblock)
boundary.y <- boundary.y/conversion factor(number depends on the dimensions
and GSD (ground sampling distance) of the cutblock)
```

11. Place points within the boundary created, with the residuals removed. If cutblock has no residual patches, holes are not necessary.

```
cutblockboundary <- owin(poly=list(x=boundary.x, y=boundary.y)
list(x=hole1x, y=hole1y), list(x=hole2x, y=hole2y)))
```

12. Plot the points within the boundary.

```
plot(cutblockboundary)
```

13. Produce a planer point processes using the coordinates of the points (i.e., dead trees) and the cutblock boundary.

```
cutblockppp <- ppp(x=data$X, y=data$Y, window=cutblockboundary)
```

14. Create a density plot for the distribution of dead trees in the cutblock and plot the image with a resolution of 2 meters.

```
cutblockdensity <-density.ppp(cutblockppp, eps=2)
image(cutblockdensity, col = terrain.colors(1024), axes=F, main=" ",
ribwid=0.1)
```

15. Create a density plot for the distance to margin of each point within the cutblock and plot the image with a resolution of 2 meters.

```
pixeldist <- bdist.pixels(cutblockboundary, eps=2)
distanceimage <- as.im(pixeldist)
image(distanceimage, col = terrain.colors(1024), axes=FALSE, main=" ",
ribwid=0.1)
```

16. Create a model without predictor variables (i.e., just an intercept) and produce an AIC (Akaike information criterion) value

```
fm1 <- ppm(cutblockppp, ~ 1)
AIC(fm1)
```

17. Create models with each of the possible predictor variables (x distance, y distance and distance to the margin)

```
Fm2 <- ppm(cutblockppp, ~ 1 + y + distance2margin, covariates = list,
(dist2margin=distanceimage))
```

18. Extract AIC

```
AIC(fm2)
```

19. Conduct a likelihood ratio test to compare nested models (e.g. is intensity contant according to a Poisson process or does it vary spatially?)

```
anova(fm1, fm2, test="Chisq")
```

20. Obtain coefficient estimates of given model

```
estimates <-coef(fm2)
```

21. Obtain standard errors of the model coefficients

```
standarderrors <-diag(sqrt(vcov(fm2)))
```

A.2 R Code and abbreviated programming notes for Chapter 3: Differential dispersion of warren root collar weevil (*Hylobius warreni* Wood) within modified forest habitats

A.2.1 Code for logistic regression, with weevil capture as the response variable (Figure 3.4).

1. Read in data

```
mr <-read.table("data.txt", header=T, sep="\t", na.strings=".")
```

2. Convert necessary variables to factors

```
mr$plot <-as.factor(mr$plot) # plots 1, 2 and 3
mr$bb <-as.factor(mr$bb) # presence of bark beetles (0/1)
mr$live <-as.factor(mr$live) # tree condition (live/dead) (0/1)
mr$habitat <-as.factor(mr$habitat) # habitat type (live habitat/dead habitat/mixed
                                     habitat)
mr$day <-as.factor(mr$day) # day of the experiment (0-28)
mr$north.south <-as.factor(mr$north.south) # north/south direction (determine by
                                             whether the tree was north or south of
                                             the release location) (0/1)
mr$capture <-as.factor(mr$capture) # weevil capture variable (the observation of
                                     capture events each trap, for each day of the
                                     experiment (0/1)
mr$density <-as.factor(mr$density) # density of weevils within each of the plot
```

3. Fit model(s)

```
fm1 <-glm(capture ~ treey + treex + day + habitat + bb + north.south,
data=mr, family="binomial")
```

4. Examine model(s).

```
anova(fm1) # conduct an analysis of variance test
summary(fm1) # examine coefficient estimates, standard errors, degrees of freedom, F
statistic, and significance levels for model and model coefficients.
```

A.2.2 Code for analysis of covariance (ANCOVA) tests that were conducted to quantify movement rate of weevils (Figure 3.5).

1. Read in data

```
mr <-read.table("data.txt", header=T, sep="\t", na.strings=".")
```

2. Convert necessary variables to factors

```
mr$plot <-as.factor(mr$plot)
mr$bb <-as.factor(mr$bb)
mr$live <-as.factor(mr$live)
mr$habitat <-as.factor(mr$habitat)
mr$day <-as.factor(mr$day)
mr$north.south <-as.factor(mr$north.south)
mr$capture <-as.factor(mr$capture)
mr$density <-as.factor(mr$density)
mr$capture <-as.numeric(as.character(mr$capture))
mr$day <-as.numeric(as.character(mr$day))
```

3. Fit model(s)

```
fm1 <- lm(ydistance ~ plot + day + plot=day, data=mr[mr$day<12,])
```

note: I only included captures during the first 12 days of the experiment.

4. Examine model(s)

```
plot(residuals(fm1) ~ fitted.values(fm1))
```

plot the residuals to determine if data is normally distributed and check for homoscedaticity.

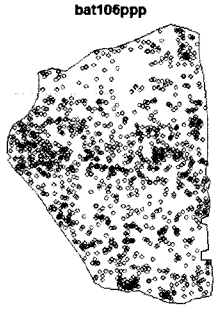
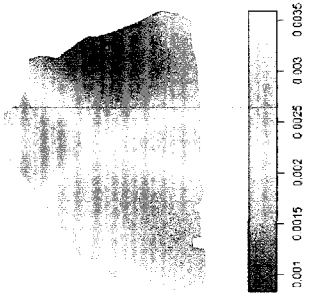
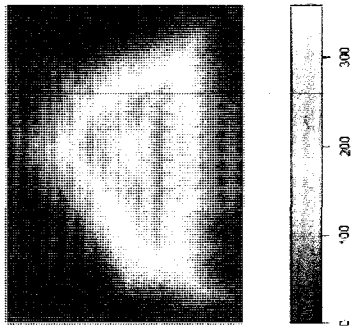
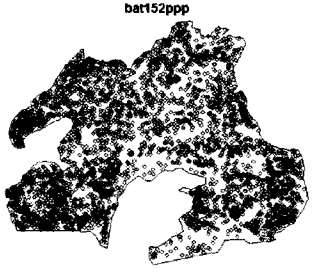
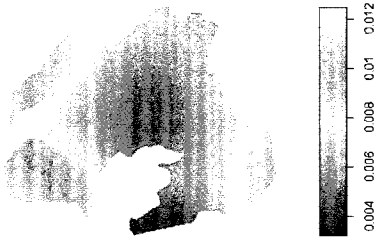
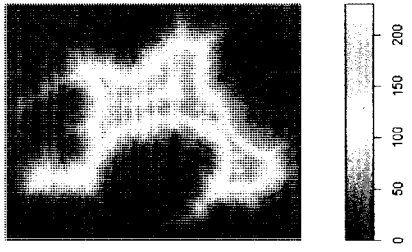
```
anova(fm1)
```

conduct an analysis of variance test.

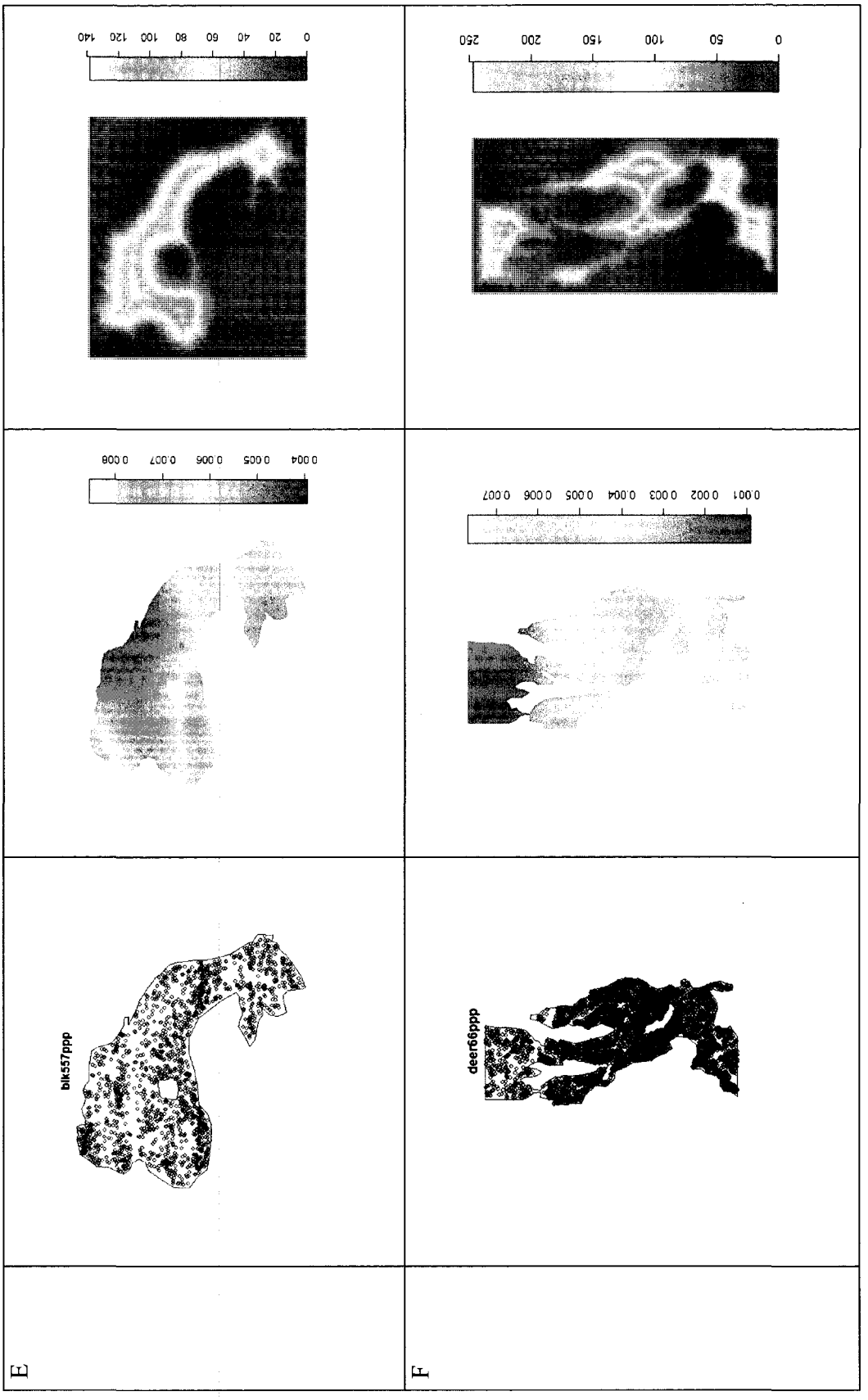
```
summary(fm1)
```

examine coefficient estimates, standard errors, degrees of freedom, *F* statistic, and significance levels for model and model coefficients.

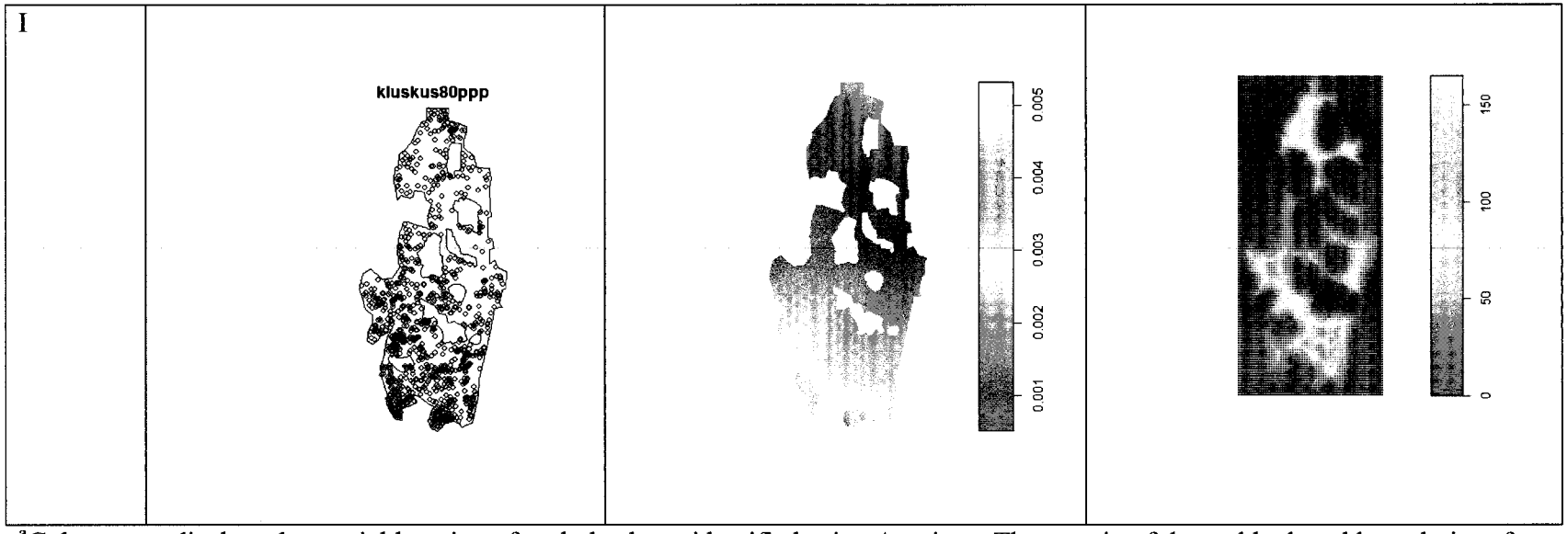
Table A.1. Cutblocks with dead trees spatially referenced using Arcview and plotted using R v.2.5.0. Locations of cutblocks are provided in Table 2.1.

Cutblock	Spatial location of dead trees[a]	Intensity of mortality surface[b]	Distance to margin surface[c]
A			
B			

C
D
salmon17ppp
0 50 100 150 200 250
0 50 100 150 200 250 300
2e-04 4e-04 6e-04 8e-04 0.001 0.0012
4e-04 6e-04 8e-04 0.001 0.0012


0 20 40 60 80 100 120 140
0 50 100 150 200 250
0.004 0.005 0.006 0.007 0.008
0.001 0.002 0.003 0.004 0.005 0.006 0.007
blk557ppp
deer66ppp
E
F

G
H
0
100
200
300
400
500
2e-04
3e-04
4e-04
5e-04
6e-04
7e-04
8e-04
bob22292ppp
bob22291ppp



[a]Column one displays the spatial location of each dead tree identified using Arcview. The margin of the cutblock and boundaries of residual plots were imported into R using shapefiles created with Arcview.
[b]Column two displays the intensity surface of mortality (λ) across each cutblock (in dead trees/m^2), green represents low intensity and yellow, red and white represent progressively higher intensities of mortality.
[c]Column three displays the distance to the margin for each plot, the green represents areas outside of the cutblock and the gradient of colour from green to yellow to red to white represents progressively farther distances from the margin.

APPENDIX B

B.1 Instructions for constructing and installing the "Björklund funnel trap"

These instructions have been modified from instructions obtained from Dr. Niklas Björklund, while he was working on a post-doctoral placement at the University of Northern British Columbia. Permission has been obtained to include these instructions.

The aim of the "Björklund funnel trap" the trap is to catch insects walking on the stem of trees. This trap is ideal for the flightless Warren root collar weevil *Hylobius warreni*, and is simple to construct and effective at capturing large numbers of weevils. No chemical lures are required, and the insects are captured alive.

The trap consists of a funnel that is attached to the lower portion of the stem of a tree. The following materials are used to construct these traps: black tar-paper (readily available from any commercial store that supplies materials for roof repairs), Fluon® (obtained from *Kristin L. Nagg, Customer Service Manager, AGC Chemicals Americas, Inc. 255 S. Bailey Road Downingtown, PA 19335, telephone number: 610-380-6258, knagg@agcchem.com*), paper clips, masking tape (5 cm wide) and packaging tape (5 cm wide).

To construct a "Björklund funnel trap", first cut out the traps according to the template shown in Figure E.1. Second, paint on the Fluon® and let the trap dry. Third, carefully pile the traps in pairs with the Fluon® -coated sides towards each other (if you get Fluon® on the outside of the trap, they will become less efficient).

To install the traps, first, wrap packaging tape around the stem a few centimetres above where you intend to attach the lower end of the trap and paint it with Fluon®. The trap should be at least a few centimetres above ground, so that the weevils first arrive to the stem and then climb the trap. The trap should also be below the first branches to ensure weevils

do not feed on lower branches and avoid being captured. If the bark is rough, it has to be smoothed by hand before attaching the trap. Wrap the paper trap around the stem so that the lower part fits tightly against the stem of the tree. Attach a paper clip on the top part of the trap to stabilize it. Attach short pieces of masking tape all around the bottom of the trap as a "skirt". Wrap a few rounds of the tape hard around the stem to firmly attach the "skirt" to the stem. The tape needs to be fastened tightly because the weevils are strong. If the trap is not tight, they will escape.

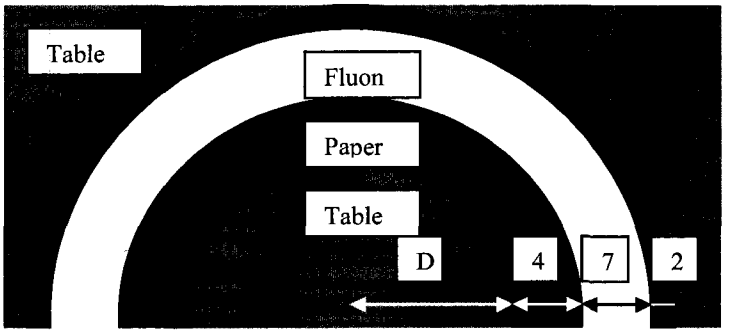


Figure B.1. Template for "Björklund funnel trap". D is the maximum diameter a tree may have that the trap can be attached to, the diameters of the fluon and non-fluon areas is measured in centimetres. (Modified from unpublished material provided by and reprinted with permission from Dr. Niklas Björklund).

APPENDIX C

C.1 Feeding behaviour of Warren root collar weevil on host and non host bark

Little is known about the feeding preferences of Warren root collar weevils. Although they feed on a variety of coniferous tree hosts (Cerezke 1994), it is not known if host preference exists. Feeding preference has been investigated with other *Hylobius* species in northern Europe (Leather et al. 1994, Månsson and Schlyter 2004, Månsson et al. 2005, Toivonen and Viiri 2006) and Wisconsin (Hunt et al. 1993).

To determine if Warren root collar weevil feeding varies across host species, I examined feeding over a 6 day period in choice and no-choice experiments. Four Warren root collar weevils used for this experiment were starved for one day prior to the experiment. The weevils were maintained prior to and during the experiment in growth chambers at 7 degrees Celcius.

Branches 100 mm in length were collected from interior hybrid spruce *Picea glauca x engelmannii*, lodgepole pine *Pinus contorta* Douglas var. *latifolia* (Engelmann) and trembling aspen *Populus tremuloides* Michx trees. The diameter of each branch was recorded at either end and at the middle of each branch. I summed the diameter for each branch and found the average diameters of branches used for the choice experiment were as follows: 2.71 mm for spruce, 2.64 mm for pine, and 2.88 mm for aspen. Similarly, the average diameter for branches used for the no-choice experiment were as follows: 2.68 mm for spruce, 2.58 mm for pine and 2.84 mm for aspen. The experiment started on 12 September 2006. In the no-choice experiment, each weevil was placed in a Petri dish (10 cm diameter) containing one food source (i.e., spruce, pine or aspen branch) and a moistened

filter paper. In the choice experiment one weevil was placed in a Petri dish (10 cm diameter) containing all three food sources (i.e., spruce, pine and an aspen branch). On 13, 15, and 18 of September 2006, I examined each branch for evidence of feeding. After the six days, I observed extensive feeding on pine and spruce branches but minimal feeding on the aspen branches used in the no-choice experiment. Feeding in the choice experiment occurred extensively on the spruce and pine branches but no feeding was recorded on the aspen branch.

These results provided preliminary evidence that adult Warren root collar weevils will feed on both pine and spruce but will not feed on aspen. These experiments were repeated in a more robust manner by Gareth Hopkins during the summers of 2007 and 2008 at the University of Northern British Columbia, while he was working on an independent study with Dr. Brian Aukema. I found similar results, showing no feeding on aspen, and reduced feeding on spruce (Hopkins et al. 2008). This work may be useful for determining recommendations for species mixes when replanting in areas prone to Warren root collar weevil-induced tree mortality.

Appendix Literature Cited

Cerezke, H. F. 1994. Warren rootcollar weevil, *Hylobius warreni* Wood (Coleoptera: Cuculionidae), in Canada: ecology, behaviour, damage relationships, and management. Canadian Entomologist **126**:1383-1442.

Diggle, P. 1985. A kernel-method for smoothing point process data. Applied Statistics-Journal of the Royal Statistical Society Series C **34**:138-147.

Hunt, D. W. A., G. Lintereur, S. M. Salom, and K. F. Raffa. 1993. Performance and preference of *Hylobius radicis* Buchanan, and *H pales* (Herbst) (Coleoptera: Curculionidae) on various pinus species. Canadian Entomologist **125**:1003-1010.

Hopkins, G. R., M. D. Klingenberg, and B. H. Aukema. 2008. Feeding and ovipositional behaviour of *Hylobius warreni* Wood (Coleoptera: Curculionidae) on host and non-host bark in laboratory bioassays. Agricultural and Forest Entomology: Accepted pending revisions.

Leather, S. R., S. I. Ahmed, and L. Hogan. 1994. Adult feeding preferences of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae). European Journal of Entomology **91**:385-389.

Månsson, P. E., C. Eriksson, and K. Sjödin. 2005. Antifeedants against *Hylobius abietis* pine weevils: An active compound in extract of bark of *Tilia cordata* linden. Journal of Chemical Ecology **31**:989-1001.

Månsson, P. E. and F. Schlyter. 2004. *Hylobius* pine weevils adult host selection and antifeedants: feeding behaviour on host and non-host woody scandinavian plants. Agricultural and Forest Entomology **6**:165-171.

R-Development-Core-Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 2-900051-07-0. http://www.R-project.org.

Toivonen, R. and H. Viiri. 2006. Adult large pine weevils *Hylobius abietis* feed on silver birch *Betula pendula* even in the presence of conifer seedlings. Agricultural and Forest Entomology **8**:121-128.